TESTING WHEN AND HOW HABITAT CASCADES CONTROL BIODIVERSITY OF MARINE BENTHIC ECOSYSTEMS

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ACKNOWLEDGEMENT

To my parents,
who have always helped me with more means than those they had available ...
To my brothers,
who have always reminded me that I never left home ...

28 October 2014

Was it worth leaving my country, my house, my flag, my family, my friends, my sea…?"

30 April 2018

It has been three years and six months since I left home and not a single day has passed without asking myself that question. But becoming a scientist has been the dream of my last 25 years and, maybe, now I am pretty close.

First of all, thanks to my father and my mother, Saro and Milly, as they have spent their entire life teaching, defending and supporting me with the largest of the existing feeling in the world and the most powerful weapon they have always been able to wield better: love for their family. Comprehension was their way to let me go where my heart wanted, allowing me to achieve much more ambitious goals than those I aimed for. Silence was their way not to make my choices weigh. Sacrifice was their way to smooth the road on my way as much as possible.

Thanks to my brothers, Carmelo and Giuseppe, who have the huge merit of always reminding me that the house was never full and the family never complete without me. And also, for having shared equally between them the burden of daily problems that we used to divide into three.

Thanks to my friends for understanding my choices and not forgetting me. Luckily, I have too many friends to mention, but I hope that everyone, in their heart, feels rightly remembered here. Nevertheless, it is necessary to mention three of them. Antonio, always a witness to all the events that have significantly marked my life, positive and negative, professional and not. Luca and Mimmo, to have lightened up my homesickness with their presence and joy.

Last but least, Mads and Dave, not as supervisors, but as scientists that believed in me and my pure passion and dedication for research. Thanks for supporting me when I thought things were stronger than me. And above all, thanks for always expecting great professional standards from me.

It has not been easy but all these people, and many others, have had a very strong influence on my life and my career over the last three and a half years. And the most important thing is that everyone, with their own way, made me understand that …

… yes!
It was really worth it!!!

ABSTRACT

The important role of indirect facilitation, like trophic cascade and keystone predation, in structuring communities have been documented over many decades and across ecosystems. By contrast, indirect facilitation mediated by habitat cascades (where 'inhabitants' organisms are facilitated through sequential habitat formation or modification) is less studied, and these processes are not covered in ecological text books or conservation practices. This could be because habitat cascades are ecologically unimportant, or, alternatively, highlights a major research gap.

In this thesis, I investigated the core hypothesis that habitat cascades can be key drivers of biodiversity in marine benthic ecosystems. To test this hypothesis, I combined descriptive and experimental field and laboratory studies aimed at improving our understanding of the mechanisms underpinning habitat cascades via three broad research objectives: (i) quantifing the variability in habitat cascades under different environmental conditions, (ii) testing mechanisms that increase or decrease habitat cascades, (i) testing how habitat cascades can be affected by human stressors.

In Chapter 2, I described two new habitat cascades from relatively 'simple' sedimentary estuarine shell beds, where small infaunal bivalves (*Austrovenus stutchburyi*, primary habitat former) provide substrate for large and form-functionally different seaweeds (*Ulva* sp. and *Gracilaria chilensis*, secondary habitat formers). To date, most research on habitat cascades has focused on interactions between a single primary and secondary habitat former studied on small spatio-temporal scales, thereby questioning if habitat cascades have broad ecological relevance. I tested if habitat cascades, when standardized by seaweed biomass, are stronger at high than low abundances of the secondary habitat former and when the secondary habitat former has high (*Gracilaria*) compared to low (*Ulva*) morphological complexity. I also tested if habitat cascades are stronger at higher latitudes, where intertidal desiccation stress is stronger, and when secondary habitat formers are alive compared to mimics. In contrast to my hypotheses, I found weaker habitat cascades at high abundances and for the coarsely branched habitat formers, and I found no patterns across latitudes; however, as expected I did find stronger habitat cascades for living than mimic of secondary habitat formers.

Chapter 3 described, from the same estuarine sedimentary system, a rare example of a 'higher-level habitat cascade'. Virtually all habitat cascade studies have tested if and how two co-occurring habitat-forming species affect biodiversity compared to systems dominated by a

single habitat-forming species. My aim here was to document a new 'long habitat formation cascade' where the primary bivalve *Austrovenus* provides attachment space for the secondary seaweed *Gracilaria*, that again provides substratum for the tertiary epiphytic seaweed *Ulva*. I tested if this long bivalve-seaweed-seaweed cascade affected mobile invertebrates and if it is a general process operating across *Gracilaria* biomasses, seasons, elevation levels, sites and estuaries. My study confirmed that *Ulva* increased invertebrate abundances and altered community structures, whereas increases in taxonomic richness only was observed under a smaller subset of environmental conditions. These positive effects were, however, not supported for non-living *Ulva* mimics, suggesting that common invertebrates graze on *Ulva*.

In Chapter 4 I described a new habitat cascade from a seagrass-dominated system where unattached seaweeds (*Ulva*, secondary habitat former) can become entrapped and entangled around seagrass leaves (*Zostera muelleri*, primary habitat former). I tested the hypotheses that (i) the presence of seaweeds entangled in estuarine seagrass beds modify biodiversity via cascading habitat formation, (ii) similar processes occur across a wide range of spatial and temporal conditions, and (iii) the biomass and the structural attributes of seaweeds (comparing living vs artificial mimics) modify the strength of habitat cascades. I found that entangled seaweeds, across latitudes, elevation levels and seasons, consistently increased the abundance and richness of invertebrates and I also found stronger facilitation of invertebrates in high than low seaweed biomass and by live than mimic seaweeds. Furthermore, an experiment, using different seaweed mimics showed consistent facilitation of invertebrates with increasing mimic biomass between estuaries and across latitudes, thereby supporting all three hypotheses in a single experiment. I concluded that entangled seaweeds, by adding biomass and different physical structures, can support strong habitat cascades in sedimentary estuarine seagrass beds.

In Chapter 5 I tested, again in a seagrass-dominated system, if and how anthropogenic stressors, like fertilization and enhanced sedimentation, affect seagrass performances and seagrass-seaweed habitat cascades. I found that fertilization had little impact whereas even low sedimentation levels had strong negative effects on both seagrass and fauna. Furthermore, I found strong negative effects of sediments, across seasons and elevation levels, but also that negative effects of sediments on invertebrates were elevated in the presence of the secondary habitat former. These results thereby provide rare evidence of how a habitat cascade can break down under high anthropogenic stress.

In Chapter 6, I studied habitat cascades from more diverse rocky intertidal shores. Primary habitat formers with different morphologies affect secondary habitat-forming epiphytes and epifauna differently. However, no studies have tested the opposite hypothesis;

do morphologically ‘similar’ congeneric primary habitat formers support similar epiphytes with similar direct and indirect cascading effects on invertebrate communities? This hypothesis was tested by sampling co-existing congeneric habitat-forming fucoid seaweeds, *Cystophora torulosa*, *C. scalaris*, and *C. retroflexa*, with and without epiphytes across reefs and latitudes. The survey was then followed by field experiments, where defaunated *Cystophora* species and the morphologically different fucoid *Hormosira banksii*, with and without living and mimics of epiphytes, were out-transplanted to quantify the impact on colonizing gastropods. I found that the three *Cystophora* species supported different gastropod communities and had different cascading effects, and that these results can be, in part, explained by their physical structures. I also found that epiphytic biomass had strong positive effect on gastropods abundances, and that artificial mimics and live epiphytes were colonized by similar gastropod communities, suggesting that structural effects are more important than whether the habitat is ‘edible’.

In Chapter 7, I tested, again from rocky intertidal systems, if habitat cascades affect secondary (animal) production. Secondary production of small mobile invertebrates inhabiting *Cystophora* seaweed, with and without epiphytes, was estimated from published productivity models. More specifically, I tested if (i) the three *Cystophora* species support similar secondary production, (ii) finely branched epiphytes increase secondary production, (iii) production is greatest in warmer locations and seasons, and (iv) secondary production is higher on living epiphytes than non-living epiphyte mimics. The first two hypotheses were rejected as the three *Cystophora* species supported different secondary production and because epiphytes, when its biomass was taken into consideration, did not increase secondary production. Nevertheless, the two latter hypotheses were both supported, as production was highest in the northern location and in summer months and on living than mimic epiphytes. Thus, similar looking congeneric primary habitat formers supported different secondary production and epiphytes did not increase secondary production per seaweed-biomass, but will increase areal-based production when epiphytes enhance total standing plant biomass.

I conclude that poorly studied habitat cascades were ubiquitous in marine benthic systems on the South Island of New Zealand, modifying animal biodiversity across habitats, seasons, years, latitudes, sites and elevations levels. I also conclude that data on the abundances, morphologies and types (live or not) of co-existing habitat formers were strong mechanistic descriptors of habitat cascades. I finally suggest that habitat cascades, like other important indirect facilitation processes, should be covered in ecological text books and conservation practices.

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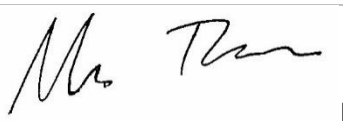
Name: Mads Thomsen Signature:  Date: 25/04/2018

CHAPTER 1: General introduction

1.1 Structuring ecological processes: habitat-forming species and habitat cascades

Most classic ecological theory has focused on negative species interactions such as predation and competition (Gause et al. 1936, Navarrete and Menge 1996, Paine 1966) but positive interactions such as facilitation, in particular through habitat formation and habitat modification, have received increasing focus in the last few decades (Bertness and Callaway 1994, Bertness and Leonard 1997, Callaway 1995, Hacker and Gaines 1997, Jones et al. 1997, Power et al. 1996, Stachowicz 2001). Although facilitation ecology has been conceptually expanded (see previous references), the majority of models of community organization do not integrate positive interactions (Bruno et al. 2003) and are usually focused on resource levels, physical stresses and negative species interactions such as predation and competition (Holt et al. 1994, Menge and Sutherland 1976, 1987, Tilman 1982, 1994, Tilman and Grace 1990) and recruitment processes (Hubbell 2001). To create conceptual models more reflective of the full range of factors that can shape natural systems, we need to incorporate and consider the relative role of positive interactions in terms of conceptual and quantitative frameworks (Bertness and Callaway 1994, Bertness and Leonard 1997, Callaway 1995, Hacker and Gaines 1997, Jones et al. 1997, Power et al. 1996, Stachowicz 2001). For example, Bruno and colleagues (Bruno and Bertness 2001, Bruno et al. 2003) hypothesized that the hierarchical structure of many communities is based on positive interactions. In these types of communities, facilitation by habitat-forming species (such as kelps, corals, trees) can be the primary interaction allowing a set of species to occupy a given habitat by reducing the environmental stress (oxygenating the soil, buffering the wave action, cooling the substrate or limiting predation). Secondary factors like competition, predation, disturbance, and recruitment then further shape community organization within the system provided by a habitat-forming species. Hierarchical organization of communities can have a prominent role in many systems, particular when considering biogenic habitat formation and modification such as in submerged aquatic vegetation, where predators and prey rely on the refuge provided by the vegetation (Heck Jr and Crowder 1991). Altieri et al. (2007) tested this hierarchical facilitation model experimentally, demonstrating that cordgrass reduces environmental stress for mussels that in turn provide stable attachment structures for intertidal invertebrates and seaweeds. Altieri referred to this empirical example as a ‘facilitation cascade’, demonstrating that entire

communities can be dependent on both direct and indirect positive interactions. Facilitation cascades refer here to a broad group of indirect facilitation processes, mediated by a different facilitation processes such as habitat formation, habitat modification and mutualism. More generally, indirect effects occur when the effect of one species on another is mediated by one or more additional species, and these processes can be pervasive in ecology (Abrams and Matsuda 1996, Menge 1995, Ohgushi 2008, Stachowicz 2001, Werner and Peacor 2003, Wootton 2002). For this reason, understanding indirect effects, and in particular indirect facilitation, can help us to create strong models that can predict and explain the responses of ecosystems to perturbations (Bolker et al. 2003, Borer et al. 2005, Borrett et al. 2010, Dambacher et al. 2002, Paine 1980). The widespread occurrence of facilitation cascades in a variety of ecosystems suggests that these processes are of general ecological importance (Angelini et al. 2011, Thomsen et al. 2018, Thomsen et al. 2010). However, compared with other types of indirect facilitations, like trophic cascades and keystone predation, they have been poorly studied (Altieri et al. 2007, Bell et al. 2014, Thomsen et al. 2010). There is therefore a growing interest in understanding when and where facilitation cascades are ecologically important (Altieri et al. 2010, Angelini et al. 2011, Bruno and Bertness 2001, Bruno et al. 2003).

1.1.1 Habitat cascades

Among the many different types of facilitation cascades, habitat cascades, where 'inhabitants' (organisms associated with a specific habitat, sometimes referred to as 'clients', 'end-users', or 'focal species') are facilitated through sequential habitat formation (Fig. 1.1-1.2), have been studied most, probably because it is easier to document habitat formation than commensalism, habitat modification or mutualism (Thomsen et al. 2010). The main focus in my thesis is on habitat cascades, and I refer to the primary and secondary interacting organisms as the primary and secondary habitat-forming species (a 'large and/or aggregated sedentary organisms that characterise a habitat'; Jones and Andrew 1992). Note, however, that other authors have used related terminology to describe these ecologically important species, like primary and secondary 'foundation species' (a species able to structure communities; Dayton 1972), 'habitat modifiers' (species able to 'alter the physical structure of the environment'; Aubry and Raley 2002), or 'ecosystem engineers' (a species able to modulate the availability of resources for other species via direct or indirect physical habitat modification; Jones et al. 1994, Wright et al. 2002). The general dependence of species diversity and abundance on habitat created by living organisms has long been recognized (Dayton 1972, Holdridge 1947, Huston and Huston

1994, MacArthur and MacArthur 1961, Whittaker 1975), but most ecological models do not explicitly recognize the wider importance of multiple co-occurring habitat-forming species, instead being focused on community interactions and ecosystem processes within a specific habitat created by a single type of habitat-forming species (Bruno and Bertness 2001, Ellison et al. 2005) (but see Angelini et al. 2011). Despite this, it has been suggested that facilitation among multiple co-occurring habitat-forming species is a widespread phenomenon of fundamental importance to community structure (Altieri et al. 2007, Angelini et al. 2011, Jones et al. 1997, Thomsen et al. 2010).

Habitat cascades are likely to be pervasive ecological processes, and should be particularly common in ecosystems where epibiosis (a 'non-symbiotic association between 'epibionts', an organism growing attached to a living surface, and 'basibionts', a substrate organism'; Wahl 1989) is widespread such as in forests (Zotz and Bader 2011) and marine benthic systems (Wahl 2009, Wernberg et al. 2010). Perhaps that is why habitat cascades have mainly been studied in a few systems dominated by large primary habitat-forming species such as tree stands (Angelini and Silliman 2014, Cruz-Angòn and Greenberg 2005, Watson 2002), salt marshes (Altieri et al. 2007, Angelini et al. 2015, van der Zee et al. 2016), seagrasses (Edgar and Robertson 1992, Thomsen 2010, van der Zee et al. 2016), and mangroves (Bishop et al. 2012, Bishop et al. 2013). It therefore remains an important goal to investigate if habitat cascades are prevalent in other habitats and ecosystems. More specifically, both experimental and comparative studies have shown that these critical organisms can have positive effects on inhabitants by creating unique refuges from biotic or abiotic stress (Altieri et al. 2007, Bishop et al. 2012, Dijkstra et al. 2012, Thomsen et al. 2016a, Thomsen et al. 2010, Yakovis et al. 2008) and by generating structures and conditions within which other species and their interactions occur (Bruno and Bertness 2001, Bruno et al. 2003, Stachowicz 2001, Thomsen et al. 2016a, Yakovis and Artemieva 2017). Consequently, co-occurring habitat-forming species can affect inhabitants by (i) modifying the abundance of individuals in the local community, (ii) affecting entire form-functional groups and/or (iii) having community-wide impacts (Polis et al. 2000).

1.1.2 Facilitation mechanisms of inhabitants

Biogenic habitat formers can facilitate inhabitants by providing food and attachment space and/or reducing stress and predation. For example, in intertidal communities in Oregon, D'Antonio (1985) demonstrated that epiphytes attached to the red alga *Rhodomela larix* provided food for snails and amphipods. Similarly, Bologna and Heck (1999) compared

artificial mimics and live epiphytes to demonstrate that *Thalassia testudinum*'s edible epiphytes supported more invertebrates compared to the mimic ones. Jones and Thornber (2010) also reported trophic benefits for inhabitants in habitat cascades supported by invasive seaweeds, where the abundance of the herbivorous snail *Lacuna vincta* was positively correlated with biomass of the epiphyte *Neosiphonia harveyi*.

In addition to trophic resources, biogenic habitat formers also provide settlement space and can reduce environmental stress. Altieri et al. (2007) demonstrated that cordgrass stabilized substrates for ribbed mussels and reduced environmental stress (through shading) whereas the mussels provided stable attachment substrate for barnacles and seaweeds. Similarly, Bishop et al. (2013) demonstrated that mangroves' pneumatophores trapped floating mats of the canopy-forming seaweed *Hormosira banksii* which, in turn, supported a diverse community of snails. Bell et al. (2014) reported positive effects of the kelp *Ecklonia radiata* on the urchin *Holopneustes purpurascens* (by providing food) which, in turn, modified the physical architecture of the kelp to protect the snail *Phasianotrochus eximius* from strong wave action. Also in sedimentary estuaries, where hard abiotic substratum such as rocks and boulders, is a limited resource and at high risk of burial by sediments over time, live shell-forming molluscs can remain on the sediment surface and provide stable settlement structures for sessile organisms (Gribben et al. 2009, Gutiérrez et al. 2003, Wahl 2009). For example, Thyrring et al. (2013) demonstrated that the invasive snail *Batillaria australis*, throughout most of Swan River Estuary in Australia, greatly increased substratum for sessile organisms. This resulted in almost 50 times more sessile individuals associated with this single invasive species compared to all native molluscs combined.

Finally, refuge from predation can be a key benefit for inhabitants as demonstrated by Leber (1985), who reported a reduced predation rate of the pink shrimp *Penaeus duorarum* across a vegetation gradient dominated by the seaweeds *Laurencia poitei* and *Digenia simplex* on a *Thalassia testudinum* seagrass bed. Similarly, in Florida, Adams et al. (2004) demonstrated that drifting seaweeds entangled on *Thalassia testudinum* seagrass leaves effectively reduce the predation rate on post-settlement *Lagodon rhomboides* by other predatory fishes. Also in the previously mentioned facilitation kelp-urchin-snail described by Bell et al. (2014), the architectural modification of the kelp structure by the urchin is likely to protect snails from predators.

1.2 Epibiosis and epiphytism as a common pre-requisite for habitat cascades

Terrestrial epiphytes are often identified as secondary habitat-forming species that facilitate communities of birds and invertebrates (Angelini and Briggs 2015, Cruz-Angòn et al. 2009, Dial et al. 2006, Ellwood and Foster 2004, Nadkarni 1994, Nadkarni and Matelson 1989, Watson 2002, Yanoviak et al. 2011, Zytynska et al. 2011). Similarly, in marine ecosystems, many small herbivores are facilitated by epiphytes that provide food (Alcoverro et al. 1997, Conlan 1994, Jernakoff et al. 1996, Jernakoff and Nielsen 1997, Kitting 1984, Klumpp et al. 1992, Kristensen 1972, Nielsen and Lethbridge 1989, van Montfrans et al. 1984), increase the structural complexity of the primary habitat-forming species (Hall and Bell 1988, Heijs 1987, Schneider and Mann 1991b) and provide additional habitat space and predation refugium (D'Antonio 1985, Pavia et al. 1999). These benefits are particularly important for organisms who preferentially select habitats with shelters that match their body sizes (Hacker and Steneck 1990, Schneider and Mann 1991a, b). Many studies involving seagrasses and attached epiphytic macroalgae have reported that an increment in habitat heterogeneity can increase species richness and density of organisms (Edgar and Robertson 1992, Lewis III and Stoner 1983, Martin-Smith 1993, Stoner and Lewis 1985). The fact that epiphytes provide additional structures suggests that their presence in these habitats would also increase the abundance of other organisms (Bologna and Heck 1999). For example, Hall and Bell (1988) found, on blades of the seagrass *Thalassia testudinum*, positive correlations between the abundance of epiphytic alga *Giffordia michelliae* as well as artificial epiphyte mimics and the abundance of meiofauna. This study provided early evidence that the pure physical structure of the secondary (epiphytic) habitat-forming species can be an important driver of habitat cascades. Shortly after, Edgar and Robertson (1992) carried out an experiment removing epiphytes from *Amphibolis* seagrass leaves resulting in fewer species and lower abundances of inhabitants. Finally, Bologna and Heck (1999) compared invertebrates associated with habitat mimics with and without natural or artificial epiphytes in a mixed seagrass bed (i.e., using mimics to represent both the primary and secondary habitat former). Abundances of many inhabitants were higher on mimics with natural epiphytes compared to mimics with artificial ones, suggesting that food subsidy for inhabitants was of some importance as a driver of this habitat cascade. In addition to experiments conducted in sandy seagrass beds, at least two studies have demonstrated the existence of habitat cascades from seaweed-epiphyte dominated rocky reefs. Martin-Smith (1993) experimentally removed epiphytes from two types of *Sargassum* seaweed mimics in Queensland, Australia. The epifaunal community composition differed between the epiphyte-

covered and the clean mimics, with higher abundances of crustaceans, polychaetes and gastropods in the presence of the epiphytes. This result was supported by Thomsen et al. (2016b), who found increasing abundances and more taxa of small mobile invertebrates with increasing biomass of the obligate epiphyte *Notheia anomala* attached to the fucoid seaweed *Hormosira banksii*.

1.3 Research gaps, core hypothesis and broad objectives

Our knowledge about habitat cascades is limited. For example, Thomsen et al. (2010), in the first review of habitat cascades, suggested that more studies should test hypotheses to increase our understanding of mechanisms underpinning habitat cascades as well as document habitat cascades from more systems and biogeographical regions. Since this early review, many studies have documented habitat cascades (Angelini and Silliman 2014, Angelini et al. 2015, Thomsen et al. 2018, Thomsen et al. 2016a, Watson 2015, Watson and Herring 2012, Yakovis and Artemieva 2017), but despite an increasing number of studies documenting habitat cascades, few have focused on (i) quantifying spatio-temporal variability of habitat cascades, (ii) underpinning mechanisms, (iii) comparing habitat cascades among different systems, (iv) measuring the effects on other responses than biodiversity, and (v) how external stressors may modify habitat cascades. In this thesis, I address these research gaps, ***testing the core hypothesis that habitat cascades are key drivers in controlling and maintaining biodiversity in marine benthic ecosystems***. To test this hypothesis, I combined descriptive and experimental field and laboratory studies aimed at improving our understanding of the mechanisms underpinning habitat cascades. This research will also help to improve conservation efforts, and aid in creating realistic conceptual and predictive ecological models that can be tested in other habitats, ecosystems and biogeographical regions. The core hypothesis was tested through three broad research objectives, where I aimed to: *(i) quantify variability in habitat cascades under different environmental conditions, (ii) test mechanisms that increase or decrease the strength of habitat cascades, (iii) test how habitat cascades are modified by human stressors and how they affect secondary production.*

These objectives were examined in three study systems characterized by fundamentally different types of primary and secondary marine habitat-forming species and widely different environmental conditions (Fig. 1.1-1.2): (i) sedimentary bivalve-dominated estuaries, (ii) sedimentary seagrass-dominated estuaries, and (iii) rocky shore seaweed beds. Each of the three study systems is described in two data chapters, where the first chapter provides detailed

information on spatio-temporal variability and underlying mechanisms and the second chapter addresses a more specific research gap related to habitat cascade ecology.

1.4 Model systems, model organisms and case studies

1.4.1 Model systems

My research was carried out on intertidal sedimentary mudflats, seagrass beds and rocky shore seaweed beds on the South Island of New Zealand. Intertidal systems are ideal models to quantify spatial and temporal variation in species interactions (Leonard 2000) because marine organisms are sensitive to temperature and desiccation stress and their communities can vary widely across spatio-temporal scales (Lewis 1964, Wethey 1983, 1984). Importantly, physiological intertidal stress can often be alleviated by the presence of other species such as intertidal algal canopies which reduce desiccation, irradiance and temperature (Davison and Pearson 1996, Dayton 1971, Garbary 2007, Menge 1978, Underwood and Denley 1984). Furthermore, due to the lack of hard substrates in sedimentary estuaries, biogenic habitat formers are often the main structural component that create benign microclimate for inhabitants and stable hard structures for settlement of sessile organisms. Compared to rocky shores, estuaries generally have lower biodiversity and are environments where manipulative experiments are simpler to set-up and maintain. Thus, estuaries are excellent systems for studies on habitat cascades. My main estuarine research was carried out in the Avon-Heathcote Estuary, in Christchurch (43°33'8.014"S, 172°44'26.422"E). Data from this estuary was supported by an extensive spatial survey where I sampled 15 additional estuaries along the East Coast of the South Island of New Zealand (from 40°S to 46°S), to test if my local findings have broader generality.

By comparison, rocky shores are characterized by higher biodiversity of both primary and secondary habitat formers and inhabitants, which make them excellent systems to test more complex hypotheses related to habitat cascades. Here, habitat cascades are less likely to control biodiversity because (abiotic) rocks with cracks and crevices provide a physical substrate for sessile and mobile species to live on or around and to ameliorate environmental stress. For example, if primary habitat formers are lost from a rocky system, secondary habitat formers are likely to attach to rocks instead, thereby maintaining a habitat for inhabitants (Wahl and Mark 1999). For the rocky shore research, most of my studies were done at Kaikoura (42°24'51.707"S, 173°42'18.472"E) but results from this study region were also compared to broader survey data, collected along 550 km coastline along the eastern coast of the South

Island of New Zealand, from Cape Campbell (41°43'36.685"S, 174°16'31.962"E) to Moeraki (45°21'31.907"S, 170°51'43.823"E).

1.4.2 Model organisms and habitat cascades

In this thesis, three different types of habitat cascades are studied in detail (Fig. 1.1-1.2).

Among shell-forming molluscs, the cockle *Austrovenus stutchburyi* (family Veneridae; hereafter *Austrovenus*) often dominates sheltered sedimentary estuaries in New Zealand (Morton and Miller 1973). In some places *Austrovenus* reach their densities of 200-300 per m^2 and as they burrow to a depth of 2-4 cm (Jones et al. 2005) they often leave their apex above the sediment surface providing attachment space for secondary habitat-forming sessile species. The sculptured shell makes it possible for this bivalve to maintain its position just below the mud surface, although some individuals may burrow deeper (Jones et al. 2005). In many places, *Austrovenus* shells represent the main hard substrate that sessile benthic invertebrates can colonize and some invertebrates are found almost exclusively on cockle shells, forming a distinctive epibiontic assemblage (Jones et al. 2011, Morton and Miller 1973, Mouritsen and Poulin 2003). Thus, *Austrovenus* represents the primary habitat former in both Chapter 2 and 3.

The seaweeds *Gracilaria chilensis* (hereafter *Gracilaria*) and *Ulva* spp. are typical biogenic habitat formers in sedimentary mud-dominated estuaries. *Gracilaria* is a coarsely branched red alga that can grow up to 25 cm long, and can be found in New Zealand estuaries year-round but often accumulates during spring in large masses (Jones et al. 2005). *Ulva* spp. (excluding tubular *Ulva* species) are sheet-forming green alga, often growing to > 30 cm (particularly in drift populations), and including several species that generally require genetic analysis to identify. Unfortunately, it was impossible to carry out detailed taxonomic and genetic analysis of my *Ulva* spp. samples, and these taxa were therefore here grouped as *Ulva* spp. (hereafter *Ulva*). In spring, *Ulva* grows rapidly, and can form drifting mats on the mud surface; on subsequent tides these mats drift to the margins and form dense aggregations (Jones et al. 2005). In this thesis, *Gracilaria* is considered a secondary habitat former attached to *Austrovenus* shells (Chapters 2-3) whereas *Ulva* has a more complex role as (i) secondary habitat former attached to *Austrovenus* shells (Chapters 2), (ii) tertiary habitat former attached to *Gracilaria* (Chapter 3), (iii) primary habitat former drifting around on mudflats (Chapter 4-5), and (iv) secondary habitat former entangled among seagrass leaves and rhizomes (Chapters 4-5).

Seagrasses are ecologically very different from seaweeds, with slower growth, clonal architecture and long-lived perennial and persistent structures. The primary habitat-forming seagrass species studied here (Chapter 4-5) is *Zostera muelleri* (hereafter *Zostera*), the only seagrass species in New Zealand (Short et al. 2007). *Zostera* beds are relatively common on sandy substrates and in estuaries (Den Hartog 1970) and are important for sediment deposition, substrate stabilization, and as substrate for epiphytic algae and micro-invertebrates (Hall and Bell 1988, Harlin 1980).

On rocky shores, three *Cystophora* species, *C. torulosa*, *C. scalaris* and *C. retroflexa* can dominate low-shore algal assemblages in semi-protected areas, like tide pools and channels. These species can grow up to 1 m (but are more typical 40-50 cm long) and can create a thick, closed canopy with their buoyant pneumatocysts on multi-branched fronds (Schiel 2006). It has previously been shown that intertidal *Cystophora* spp. can facilitate other intertidal understory species, largely by reducing desiccation stress during low tide (Schiel 2006). In this thesis, *Cystophora* species are considered as primary habitat formers whereas epiphytic seaweeds are secondary habitat formers (Chapters 6-7).

Among the inhabitant invertebrates, I focused on snails and crabs. Snails within the genus *Diloma* and *Micrelenchus* are common between low- and mid-tide level throughout estuaries in New Zealand and are often found around seaweeds, which represent their diet, or *Zostera* (Jones et al. 2005). Crabs belonging to the genera *Halicarcinus*, *Hemigrapsus*, *Austrohelice*, *Cyclograpsus* and *Macrophthalmus* are also common in estuaries throughout New Zealand. Crabs were sometimes classified as juveniles vs adults, because I hypothesized that these two life stages inhabited different habitat formers. For example, different crab species may use seaweeds for food or avoiding predators and intertidal stress and this habitat usage may change as the crab grows larger. Finally, for the rocky shore habitat I focused on invertebrates between 250-1000 µm. I focused on snail communities because these organisms are important epifauna on seaweeds (Siciliano unpubl. data, Cowles et al. 2009, Taylor 1998a, b, Thomsen et al. 2016b), are a heterogeneous group with different ecological functions (Chapman and Underwood 2008) and represent the wider intertidal invertebrate communities (Chapman and Underwood 2008, Smith 2005).

1.5 Thesis overview

This thesis consists of a general introduction, six data chapters investigating the role of habitat and facilitation cascades from three different ecosystems (Fig. 1.1-1.2), a general discussion,

and three appendices. The first two data chapters address relatively simple, low-diversity sedimentary bivalve-dominated estuaries (Chapters 2-3), followed by two chapters on ecologically more diverse seagrass beds (Chapters 4-5). The final two data chapters explore habitat cascades in high-diversity rocky shore seaweed beds (Chapters 6-7). Chapters 2, 4, 6 and 7 were written as traditional thesis chapters, whereas chapter 3 and 5 were written as manuscripts and submitted to *Journal of Experimental Marine Biology and Ecology* (on 18/03/2018) and *Marine Ecology* (on 15/01/2018), respectively (with second and third authors DR Schiel and MS Thomsen). The remaining four thesis data chapters will be shortened and submitted to peer-reviewed journals at a later stage. Each chapter consists of (i) spatio-temporal surveys (e.g., across latitudes, seasons and sites), providing a general overview of the habitat cascades for each system, (ii) factorial experiments, testing for mechanisms, and (iii) morphological analysis of the co-occurring habitat-forming species, to examine possible linkage between structural complexity of habitat formers and facilitation of inhabitants.

Chapter 2 describes habitat cascades from topographic simple sedimentary estuarine shell beds, where relatively small infaunal bivalves (primary habitat formers) provide attachment substrate for larger and form-functionally very different seaweeds (secondary habitat formers). The aim here is to test if this habitat cascade is affected by the biomass of the secondary habitat former and if different secondary habitat-forming species facilitate invertebrates differently. A key characteristic of this cascade is the striking ecological and morphological difference between the primary and the secondary habitat formers (bivalve vs seaweeds). Here, I expected a strong cascade because the secondary habitat-forming seaweed provides novel functions that are absent from the primary habitat former (e.g., sheltering within seaweed fronds, moisture retention, additional settlement space, etc.).

Chapter 3 also addresses sedimentary bivalve-dominated estuaries but describes a rare example of a 'higher-level habitat cascade' where the secondary habitat-forming seaweed provides attachment space for a tertiary habitat-forming seaweed, with potentially more complex effects on invertebrates. Here, I expected only minor additional facilitation effects from the tertiary habitat-forming seaweed because functions provided by this organism are likely to be partially redundant compared to the functions already provided by the secondary habitat-forming seaweed. To date, there are only three published case studies of 'long habitat cascades' but I believe they are common and widespread and should be investigated more.

Chapter 4 describes a very different type of habitat cascade where secondary habitat-forming drifting seaweed becomes entangled in seagrass beds. In this cascade the drift seaweed is not physically attached to the seagrass. Interactions between seagrass and drift algae are

typically analysed within a context of competition, but could potentially result in facilitation of invertebrates. Compared to Chapter 2, the primary and secondary habitat formers are more similar (similar sizes and both primary producers), and therefore likely to provide relatively similar levels of shelter, resources, and stress buffering. I therefore expected weaker effects of the secondary habitat former compared to Chapter 2.

Chapter 5 focuses on the same seagrass-seaweed habitat cascade but, more specifically, provides a rare test of how anthropogenic stressors (nutrient enrichment and sediment pollution) can modify the impact of the habitat cascade on the associated inhabitants. Here, I expected that anthropogenic stress would decrease the abundance of the primary and/or secondary habitat former and thereby break down the habitat cascade.

Chapter 6 describes habitat cascades from highly diverse intertidal rocky shore seaweed beds, where large canopy-forming brown seaweeds provide habitat to smaller epiphytic seaweeds (representing primary and secondary habitat formers, respectively). More specifically, I take advantage of the high diversity of co-existing habitat formers to test if facilitation from morphologically and genetically closely related primary habitat formers has similar impacts on snail-communities (a diverse model community where morpho-types are relatively easy to identify), and if these habitat cascades result in weaker effects compared to Chapter 2-5 (because of functional redundancy).

Finally, in Chapter 7 I test, in the same rocky shore seaweed-dominated system, how secondary (animal) production (instead of biodiversity) is affected by habitat cascades. Compared to the previous chapters and the published literature on habitat cascades, where typical responses are animal abundances, richness and multivariate community structure, here I estimated the effects on secondary production, measured as a function of animal abundances, body biomass, water temperature and published allometric equations. In contrast to Chapter 6 (that only examined impact on the snail community) I estimate secondary production by including all invertebrate taxa because the whole community offers a more realistic prediction of secondary production compared to the gastropod community alone.

Three appendices supplement the six data chapters. In appendix 1 I describe an experiment where I tested how all the habitat-forming species (living and mimics) studied in chapters 2-7 affect abiotic variables (temperature, light and water loss) by simulating a falling tide. This appendix thereby identifies a potential underpinning mechanisms to better understand why inhabitants respond to different biogenic structures. Appendix 2 is a published paper, where I described, with collaborators, a sixth-order habitat cascade. This paper provides a rare example of a habitat cascade composed of more than two co-occurring habitat-forming

species (see also Chapter 3) and supplements my independent Ph.D. research on habitat cascades, presented in Chapters 2-6. Finally, Appendix 3 contains supplemental material (tables, figures and pictures) related to the six data chapters.

Figures

Figure 1.1 Comparisons of biogenic habitat formers and habitat cascades studied in this thesis. The straight arrow represents the expected strength of inhabitant facilitation. '*Cystophora* spp.' includes *C. retroflexa, C. scalaris* and *C. torulosa* (represented by the brown, blue and green colour variations) whereas 'Epiphytes' includes *Jania micrarthrodia*, *Polysiphonia decipiens* and other small seaweed epiphytes.

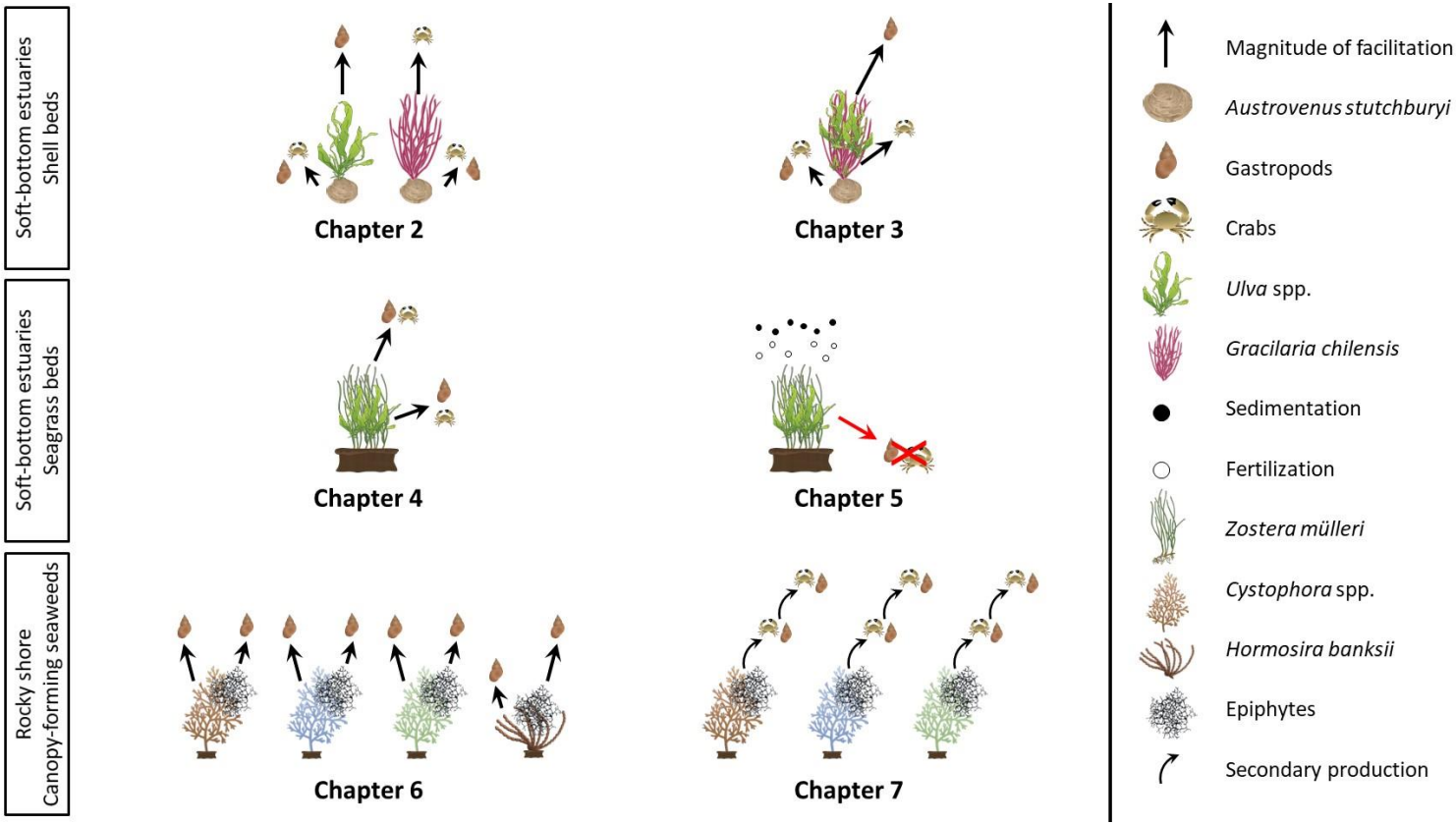
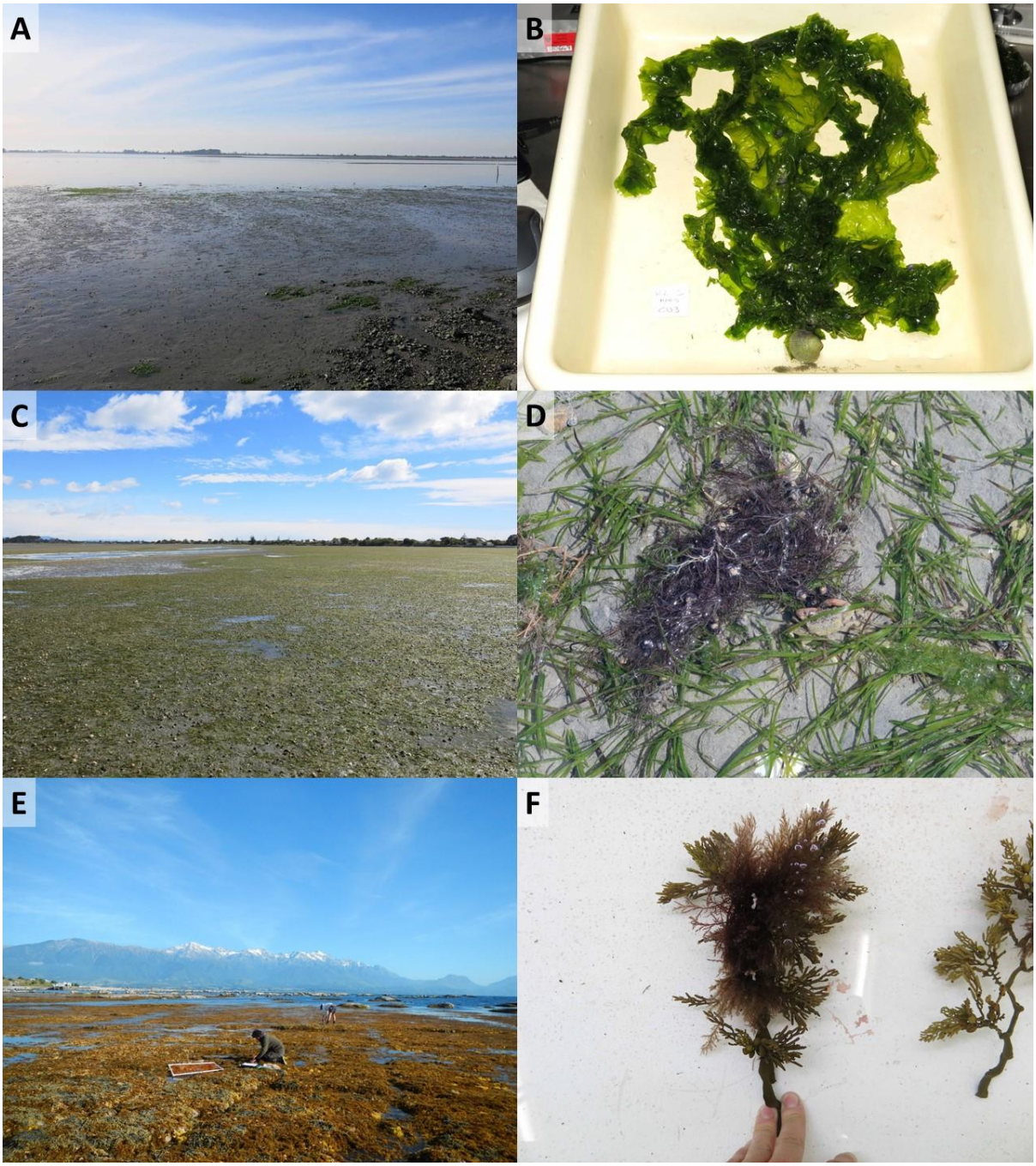


Figure 1.2 Landscape photos and close-ups of habitats and habitat cascades studied in this thesis: sedimentary mudflats with *Ulva* sp. (A, B), sedimentary seagrass beds with *Zostera muelleri* (C, D) and rocky shore seaweed beds with *Cystophora* spp. (E-F).



CHAPTER 2: The role of multiple secondary habitat-forming seaweeds in facilitating estuarine invertebrate communities

2.1 ABSTRACT

Shell-forming molluscs can be primary habitat-forming species with wide-ranging effects on the structure of invertebrate assemblages in sedimentary estuaries. These shells provide hard substratum for seaweeds to attach to, and the seaweeds can subsequently provide a secondary habitat to seaweed-associated invertebrates, giving rise to habitat cascades. To date, most research on habitat cascades has focused on interactions between a single primary and secondary habitat former, and habitat cascades are typically studied on small spatio-temporal scales. Here I examine if these habitat cascades have broad ecological relevance and underpinning mechanisms that control them. First, I tested if habitat cascades, when standardized by seaweed biomass, are stronger at high than low abundances of the secondary habitat former and when the secondary habitat former has high (*Gracilaria chilensis*) compared to low (*Ulva* sp.) morphological complexity. I also tested if habitat cascades are stronger at higher latitudes where intertidal desiccation stress is stronger, and when secondary habitat formers are alive compared to mimics, because live habitat formers can provide both structural protection and trophic subsidies. In contrast to my hypotheses, I found weaker habitat cascades at high abundances and for the coarsely branched habitat formers, and I found no patterns across latitudes. However, as expected I did find stronger habitat cascades for living than abiotic secondary habitat formers. My results confirm that habitat cascades are common within and between estuaries and seasons on the South Island of New Zealand, but also that the strength of specific habitat cascades can be idiosyncratic, vary widely between seasons and estuaries, and vary depending on what type of invertebrates dominate in an estuary. Clearly, more work is needed before the strength of estuarine habitat cascades can be predicted with confidence, particularly in relation to how individual invertebrate species that dominate in specific estuaries may have widely different affinities for primary and secondary habitat formers.

2.2 INTRODUCTION

Sedimentary estuaries are simple but stressful ecosystems, where biogenic habitat formers, like shells and seagrass, create hard structures for settlement of seaweeds and other sessile organisms (Albrecht and Reise 1994, Boström and Bonsdorff 2000, Kochmann et al. 2008,

Mouritsen and Poulin 2003, Thomsen et al. 2012b). Shell-forming molluscs are particularly important because their shells provide long lasting physical structures to which epiphytic seaweeds can attach. These seaweeds may potentially facilitate mobile invertebrates (here also referred as 'inhabitants') by providing shelter from predators and abiotic stress and a food resource (Norkko et al. 2000, Nyberg et al. 2009, Thomsen et al. 2016a, Wilson et al. 1990b), thereby giving rise to habitat cascades (sensu Thomsen et al. 2010), a common form of facilitation cascade that emphasizes sequential biogenic habitat formation. It has previously been shown that bivalves can facilitate seaweeds and invertebrates by providing hard substrates in soft-bottom habitats (Albrecht and Reise 1994, Kochmann et al. 2008, Thomsen et al. 2016a, Thomsen et al. 2010, Yakovis and Artemieva 2017). In New Zealand, for example, the dominant cockle, *Austrovenus stutchburyi*, facilitates the green sheet-forming seaweed *Ulva* sp., which in turn provides habitat for invertebrates, like snails and crabs (Thomsen et al. 2016a).

There is growing interest in predicting the strength of habitat cascades, analogue to research on trophic cascades (Borer et al. 2005). For example, it has been suggested that the strength of habitat cascades increases with (i) the amount of the secondary habitat former, (ii) its form-functional difference between the primary and secondary habitat former, and (iii) the affinity of clients for the secondary over the primary habitat former (also referred to as the Amount-Difference-Affinity hypothesis, ADAH; Angelini and Silliman 2014, Thomsen et al. 2016a, Thomsen et al. 2010). Furthermore, it has long been known that facilitation is important at both high and low stress levels, through mechanisms of habitat amelioration and predator-protection, respectively (also referred to as the Stress Gradient Hypothesis, SGH; Bertness and Callaway 1994). Subsequently, the SGH has been adopted to explain habitat cascades (Altieri et al. 2007, McAfee et al. 2016). Specifically, the SGH hypothesizes that under highly stressful conditions, facilitation is more important than negative species interactions such as competition or predation (Bertness and Callaway 1994, Bertness and Shumway 1993). I therefore expect that habitat cascades are stronger towards lower latitudes and in warmer summer months, where intertidal mudflats experience more stressful temperature conditions during low tide (McAfee et al. 2016).

Although many studies have compared different seaweed species to test how different morphologies affect associated invertebrates (Cacabelos et al. 2010, Chemello and Milazzo 2002, Hacker and Steneck 1990, Torres et al. 2015, Veiga et al. 2014, Wernberg et al. 2013), few studies have compared habitat cascades from the same ecosystem and locality with ecologically and morphologically different secondary habitat formers (Bishop et al. 2009,

Hughes et al. 2014) or have used mimics of the habitat formers to test the effects of morphology on local invertebrates (but see Bologna and Heck 1999, Schneider and Mann 1991b).

In this study, I compare two habitat cascades that can exist side by side in sedimentary estuaries throughout the world, where bivalves may provide habitat to either sheet-forming seaweeds like *Ulva* spp. or morphologically coarsely branched algae like *Gracilaria* spp. (Muta Harah et al. 2014, Nyberg et al. 2009, Scheibling et al. 1990, Seaborn 2014, Terada and Ohno 2001, Thomsen et al. 2010). More specifically, in New Zealand, *Austrovenus stutchburyi* (hereafter *Austrovenus*) is a dominant bivalve of sheltered soft-sediment shores (Morton and Miller 1973) and in some places its shell represents the only hard substrate on which benthic organisms can settle. *Austrovenus* is often colonized by various *Ulva* species (hereafter *Ulva*) and *Gracilaria chilensis* (hereafter *Gracilaria*) (Hawes and Smith 1995, Rainer 1969, Thomsen et al. 2016a, Thomsen et al. 2007). *Ulva* is an opportunistic ephemeral fast-growing green alga composed of only two cell layers, capable of rapid colonization but also considered susceptible to grazing (Littler and Littler 1980, Rosenberg and Ramus 1982, Vermaat and Sand-Jensen 1987). *Gracilaria* is a perennial red alga (Jones et al. 2005) with slower growth and a more complex multi-layered cylindrical cortex and medulla. *Gracilaria* is often more resistant to environmental stress and less susceptible to grazing (Thomsen and McGlathery 2007).

The aim of this study is to quantify the variability in habitat cascades supported by these two morphologically different secondary habitat formers. More specifically, I tested if: (i) *Gracilaria* supports higher diversity and abundances of invertebrates because it is structurally more complex than *Ulva*; (ii) herbivorous invertebrates are more abundant on the more edible *Ulva* whereas species that are susceptible to predation (like slow-moving juvenile crabs) are more often associated with the morphologically complex *Gracilaria*; (iii) above effects are stronger in warmer northern regions and (iv) in summer months and at higher elevation levels because intertidal desiccation stress is more severe under these conditions (and partly because metabolic processes, feeding and predation rates are higher in warm and cold temperate conditions); (v) living secondary habitat formers have higher abundance and diversity than non-living habitat formers (artificial mimics) because living habitat formers simultaneously provide a food source and a place to avoid predators and stress, whereas non-living mimics only provide habitat to avoid predators and stress; (vi) *Gracilaria* provides a better shelter from predation compared to *Ulva*. The first two hypotheses were tested with data from the Avon-Heathcote Estuary, in New Zealand, based on a seasonal survey, where I collected samples from different locations and elevation levels, and a field experiment. The third and forth hypothesis (and, again, the first two) was tested in a large spatial survey in 16 estuaries scattered

around three latitudinal bands on the South Island of New Zealand. Finally, the fifth and sixth hypotheses were addressed with a manipulative 'mimic' experiment and a predation field experiment, carried out in the Avon-Heathcote Estuary.

2.3 MATERIALS AND METHODS

2.3.1 Study region

A large-scale spatial survey was conducted in 16 estuaries along a latitudinal gradient, spanning 6 degrees (40°S to 46°S) of the South Island of New Zealand (Appendix 3-2.1 for a list of estuaries, geocoordinates, sample dates, and number of sampled replicates for different treatments). This survey was supplemented by a seasonal survey and three experiments conducted in the Avon-Heathcote Estuary, where *Gracilaria* and *Ulva* are commonly attached to *Austrovenus*. *Austrovenus*, *Gracilaria* and *Ulva* were common in most of the 16 sampled estuaries, except I did not find *Ulva* in Dowling Bay or *Austrovenus* (with and without attached seaweeds) in Portobello Bay, Papanui Inlet and New River. In addition, three experiments were carried out in the Avon-Heathcote Estuary, on bare mudflats in the mid-intertidal zone. Two experiments tested if invertebrate communities varied between species identities and biomass of the secondary habitat-forming seaweeds and whether primary and secondary habitat formers were alive or not. These experiments were run in the southern part of the Avon-Heathcote Estuary (Mount Pleasant suburb). A third experiment tested if seaweeds reduce predation by crabs on gastropods. This experiment was carried out in the eastern area of the Avon-Heathcote Estuary (Tern/Plover St.) away from public interference.

2.3.2 Spatial survey: effects of seaweed species identity and biomass across latitudes

A large scale spatial survey was carried out in 16 estuaries of the South Island of New Zealand between February and October 2016, representing three different latitudes: north (40°S-41°S), central (43°S) and south (45°S-46°S) (Appendix 3-2.1). The survey design was: 2 species of secondary habitat-forming seaweed (*Ulva* vs *Gracilaria*) × 2 biomasses of the secondary habitat formers (low vs high) × 2 elevations (intertidal vs shallow subtidal) × 3 latitudes (North vs Central vs South) × 4-6 estuaries per latitude × 3 replicated samples within each estuary. For each estuary and elevation level I also collected 'control' *Austrovenus*, without any attached seaweed. Cockles with or without attached seaweeds were collected with a swift movement (Alkarkhi et al. 2008, Baudrimont et al. 2003) and rapidly transferred to sealed plastic bags, to minimize loss of mobile invertebrates. All cockles with or without *Ulva* and

Gracilaria were collected in close proximity to each other (1-20 m) to ensure associated invertebrates had experienced similar environmental conditions (e.g., currents, temperature and salinity). Subtidal samples were collected just below the lowest low tide level, whereas intertidal samples were collected in the mid-tidal region. High and low biomass of seaweeds were collected by targeting seaweeds with large and dense fronds (> 6 cm frond length; *Ulva*: 0.85 ± 0.07 gDW, n = 62; *Gracilaria*: 1.54 ± 0.16 gDW, n = 67) or small and sparse fronds (< 6 cm frond length; *Ulva*: 0.11 ± 0.01 gDW, n = 69; *Gracilaria*: 0.20 ± 0.02 gDW, n = 73). Samples were stored on ice in the field before being transported to the lab for processing.

2.3.3 Seasonal survey: effects of seaweed species identity and biomass across seasons

Samples were collected in December and March (2014-2015) for the warm season and in May and August (2015) for the cold season from the southern part of the Avon-Heathcote Estuary (Mount Pleasant suburb). I collected individual *Austrovenus* buried in the sediment with attached seaweeds with the following sampling design: 2 species of secondary habitat formers (*Ulva* vs *Gracilaria*) × 2 biomasses of secondary habitat formers (low vs high) × 2 elevations (intertidal vs subtidal) × 2 seasons (warm summer vs cold winter) × 12 replicates. For each season and elevation level I also collected 'control' *Austrovenus* without any attached seaweed. Samples were collected using the same procedure as described for the survey.

2.3.4 Experiment 1: effects of seaweed species identity and biomass across seasons

Austrovenus was first collected with large fronds of *Ulva* or *Gracilaria* attached. Seaweed fronds were then pruned with a pair of scissors to represent different biomass (0.5, 5 and 25 cm frond length; *Ulva*: ca 0.30, 0.34 and 0.90 gDW; *Gracilaria*: 0.22, 0.50 and 1.32 gDW). Each cockle and seaweed frond was shaken and rinsed to remove mobile inhabitants before being transplanted into plots surrounded by 20 cm deep metal frames that prevented lateral movement (immigration and emigration) of cockles (De Montaudouin 1996). Transplantations were done at different elevations, sites and seasons in the following orthogonal experimental design: 2 species of secondary habitat formers (*Ulva* vs *Gracilaria*) × 3 biomass of secondary habitat formers (low, medium, high) × 2 elevations (intertidal vs shallow subtidal) × 2 sites (ca 3.2 and 3.8 km from the Avon-Heathcote river mouth) × 2 seasons (warmer month in March 2016 vs colder month in May 2015) × 5 replicates. Elevations and sites were similar to the seasonal survey. Each sub-experiment ran for 4 weeks and was maintained weekly by replacing a few missing cockles or cockles with damaged seaweed fronds. At the end of the experiment, all cockles were collected as in the surveys.

2.3.5 Experiment 2: effects of structure vs being alive

In the second experiment I tested if the invertebrate community differed between live and non-living analogues of the primary habitat-forming shell and secondary habitat-forming seaweed. The experimental design was: 3 types of primary habitat formers (alive cockle, cockle shell, plastic mimic) × 2 species of secondary habitat formers (*Ulva* vs *Gracilaria*) × 2 types of secondary habitat formers (living vs plastic mimics of *Ulva* and *Gracilaria*) × 3 replicates. Living cockles, empty shells and live seaweeds were collected from the Avon-Heathcote Estuary. The empty shells (still connected with their hinge) were dried at 55°C for 72 h. A 3D model of a typical live *Austrovenus* shell (35 mm length) was created by taking 78 photos from different angles covering the entire shell and stitching the photos in Autodesk Memento. Plastic mimics were printed with a Da Vinci 1.0A 3D printer (in 30, 32 and 35 mm length to mirror small size variability observed for live cockles). These mimics are morphologically (and colorwise) very similar to both live cockles and dead shells, but are constructed from plastic instead of calcium carbonate. Seaweed mimics were constructed from green plastic flagging tape mimicking the sheet-forming *Ulva*, and from red/white plastic twine, cut, twisted and wrapped to provide a shape that mimicked the coarsely branched *Gracilaria* (Appendix 3-2.7). Live and mimic seaweeds were attached to the shells with a piece of plastic twine glued on the surface of each shell (Araldite Two Part Epoxy glue). An additional piece of plastic twine was attached to a u-bent 20 cm metal peg inserted into the mud to prevent the loss of the samples from tidal currents and waves. A ca 20 cm long seaweed frond was attached to each shell, corresponding to 0.80 ± 0.18 gDW for *Ulva*, 0.84 ± 0.35 gDW for *Gracilaria*, 1.60 ± 0.00 gDW for *Ulva* mimic and 1.50 ± 0.01 gDW for *Gracilaria* mimic. In the field, shells and attached seaweeds were gently inserted into the sediment using a syringe with the apex cut to make a little hole where the shell was placed and partially covered with 50 mm sediment (simulating the natural position in the sediment of live cockles). The experiment ran for 3 weeks (mid-January to mid-February 2017) and was maintained weekly by replacing a few lost shells and seaweed fronds. At the end of the experiment, shells and seaweed fronds were collected as in the surveys.

2.3.6 Experiment 3: effects of predators

Finally, a field experiment tested if seaweed reduces crab predation on snails and, more specifically, if predation depends on the biomass and morphology of the seaweeds. Thirty cages were set up on a mudflat in the eastern part of the Avon-Heathcote Estuary (Tern/Plover St.). The experimental design was as follows: 2 predator levels (± 1 adult crab) × 5 habitats (mud

alone and with either *Ulva* or *Gracilaria* in low and high biomass) × 3 replicates. The cages were constructed from plastic containers (17×17×18 cm) with the bottom cut off (so the cage could be pushed 12 cm into the sediment, allowing 5 cm to protrude above the sediment surface). I drilled 36 1-mm holes in the side walls of the containers, to allow water levels in the cages to follow the natural tidal cycle. I added 13 *Micrelenchus tenebrosus* as the prey gastropod (8.26 ± 0.15 mm length) to each cage and one *Hemigrapsus crenulatus* as predatory crab (25.89 ± 0.49 mm carapace width) to the predator-treatments. Finally, ca 2.7 gWW and ca 3.7 gWW of *Ulva* and ca 6.0 gWW and 10.0 gWW of *Gracilaria* were added to low and high biomass treatments. Finally, cages were covered with 1-mm mesh to prevent predators and prey escaping. The experiment ran for 5 days in January 2017 and treatments were checked every 2 days monitoring if crabs and snails were alive or dead. At the end of the experiment, the number of snails crushed and the position of alive snails were recorded (attached to mud, *Ulva* or *Gracilaria*; no snails were attached to the cage walls).

2.3.7 Morphological traits of habitat formers

I also quantified morphological traits of the different habitat-forming species. Traits included surface area:dry weight ratios, fractal dimension, circularity (a measure of 'roundness', ranging from 0 for an infinitely elongated polygon, to 1 for a perfect circle; Sedgewick 2010) and lacunarity (Ferreira and Rasband 2012, an index of 'gappiness' or 'visual texture', considered a measure of heterogeneity; Karperien 2007). Ten individuals of live and mimic *Austrovenus*, *Ulva* and *Gracilaria* were blotted three times with paper towel and spread out on a white background to enhance the contrast for subsequent image analysis. For each sample a photo was taken with a Canon PowerShot G7X Mark II using flash and with ruler as a scaling reference. Each frond was then dried at 55°C for 48 h or until no further weight loss could be detected and its dry weight measured on a scale with three digits. Photos were converted to grey scale and thresholded to binary images in Photoshop whereafter traits were calculated in ImageJ (Rasband 1997-2016) with the plugin FracLac (Karperien 1999-2013).

2.3.8 Laboratory analysis

Each sample was rinsed in a 250 μm sieve to retain invertebrates associated with the different habitat-forming species. Seaweeds were detached from the cockle and weighed after drying at 55°C for 48 h or until no further weight loss could be detected. Cockles were placed in foil trays and weighted after drying at 55°C for 72 h. A few invertebrates with high affinity for cockle shells (barnacles, limpets and a sea anemone) were counted separately from mobile

invertebrates. Conspicuous taxa were identified to species whereas smaller inconspicuous species were identified to Order or Family, under a dissecting microscope at 40× magnification, and preserved in 70% ethanol.

2.3.9 Statistical analysis

I found very few invertebrates associated with cockles alone compared to cockles with attached seaweed (Table 2.2). Statistical and graphical analyses therefore only included the cockle-seaweed samples. Treatment effects were tested on (i) total abundance, (ii) taxonomic richness and (iii) multivariate structure of invertebrate assemblages. Prior to analysis data were standardized to unit seaweed biomass to remove obvious habitat-area effects (Davenport et al. 1999, Gestoso et al. 2010, 2012; see Discussion for details, Wikström et al. 2006) and square-root transformed to reduce the importance of a few highly abundant taxa and decrease variance heterogeneity. I excluded the biomass of the cockle itself from statistical analyses because its dry weight was order of magnitude higher than the seaweeds and because, as noted above, very few invertebrates were associated with cockle itself. Response variables were analyzed with permutational-based factorial analysis of variance (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994). Assumptions of normality and homogeneity of variances in the data sets were met. Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. For the seasonal survey and experiments, all factors were treated as fixed. For the spatial survey, I included only one survey from the Avon-Heathcote (the closest in time to the spatial survey). All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Results were considered significant if $p \leq 0.05$. Host-affinities were calculated from surveys and the first experiment, re-classifying abundances of different taxa (standardized to unit seaweed biomass) into seven groups with different ecologies: gastropods other than trochids, trochids, crabs other than *Halicarcinus whitei*, the crab *Halicarcinus whitei*, juvenile crabs (smaller than 5 mm), amphipods and copepods, and other invertebrates (isopods, worms, bivalves, chitons, ostracods). These data were square-root transformed and analyzed with a single factor PERMANOVA to compare invertebrates associated with *Ulva* vs *Gracilaria*. Data from the field predation experiment (percentage of gastropods consumed and their habitat preferences) were analyzed with contingency tables and chi-square tests. I also tested, using Spearmans' rank correlation coefficient, for relationships between *Ulva* and *Gracilaria* biomass, pooling all survey and experimental data, with invertebrate abundances and richness (i.e., this analysis was not standardized by seaweed biomass). Finally, morphological trait data were analyzed

individually with ANOVA and in concert with PERMANOVA, to test if traits differed between different primary and secondary habitat-forming species. All morphological data were square-root transformed and data for multivariate analysis were also normalized. Significant effects from ANOVA were followed by post-hoc pair-wise t-tests (Anderson et al. 2008).

2.4 RESULTS

2.4.1 Spatial survey: effects of seaweed species identity and biomass across latitudes

Invertebrate abundance. The most abundant taxa in the spatial survey were amphipods (3,833 individuals), followed by the two trochid gastropods *Micrelenchus tenebrosus* (1,067) and *Diloma subrostrata* (274), and the crab *Halicarcinus whitei* (262).

Eight higher order interactions were significant where Elevation × Estuary explained most of the data variability ($\eta^2 = SS_{Explained}/SS_{Total}$; $\eta^2 = 9\%$; $p = 0.001$, Table 2.1). Seaweed species identity and biomass interacted with Estuary ($p < 0.05$, $\eta^2 = 5\%$) and Elevation ($p < 0.05$, $\eta^2 = 1\%$) and, individually, interacted with Elevation and Latitude ($\eta^2 = 4\%$ total). The Species × Estuary and Species × Latitude interactions were also significant ($p < 0.01$, $\eta^2 = 7\%$ in total), highlighting that significantly more invertebrates were associated with *Ulva* compared to *Gracilaria* in central and southern regions (Fig. 2.1B-C) and, for *Ulva* samples only, more invertebrates were found in southern and central compared to northern regions (South = Central > North, Fig. 2.1A-C). Among the single test factors, Estuary explained most of the data variability ($\eta^2 = 12\%$). There were also significantly more invertebrates associated with *Ulva* fronds than *Gracilaria* (68.29 ± 7.26 ind. gDW seaweed^{-1} vs 39.35 ± 3.74) and more invertebrates in the subtidal compared to the intertidal zone (70.21 ± 7.55 vs 38.23 ± 3.36).

Invertebrate richness. Six interactions were significant (Table 2.1), including the highest 4-factor interaction ($p < 0.05$, $\eta^2 = 1.5\%$) and the three-factor interaction Species × Elevation × Estuary ($p < 0.05$, $\eta^2 = 2.4\%$). However, the 2-factorial Elevation × Estuary interaction explained most of the data variability ($p = 0.001$, $\eta^2 = 5.6\%$). The interaction Biomass × Estuary was also significant ($p < 0.05$) showing that seaweeds in low biomass, in most, but not all, estuaries were inhabited by more taxa compared to seaweeds in high biomass. A significant Species × Latitude interaction ($p < 0.05$, $\eta^2 = 3\%$) showed that *Ulva* was inhabited by many more taxa compared to *Gracilaria* in southern and central regions (Fig. 2.1E-F) and that *Gracilaria* samples from northern regions was inhabited by more taxa than central and southern regions (Fig. 2.1D-F). All single factor effects, except Elevation, were significant, with

Biomass explaining most of the data variability (η^2 = 25%). These results highlight that *Ulva* typically was inhabited by more taxa than *Gracilaria*, and that seaweeds with low biomass (per gram seaweed) were inhabited by more taxa than large ones (Fig. 2.1D-F).

Invertebrate community structure. Community structure was significantly affected by 11 interactions (Table 2.1), where the 2-factorial Species × Estuary interaction explained most of the data variability (η^2 = 6%). Both Species and Biomass interacted significantly with Estuaries, Elevation and Latitude ($p < 0.05$) but each of these interactions explained very little of the data variability. All the single test factors were also significant ($p = 0.001$), where Estuary (η^2 = 26%) and Latitude (η^2 = 7%) explained most of the data variability (Fig. 2.2). The MDS ordination did not show a clear separation between species and biomass treatments. Most of the multivariate variability was explained by amphipods, *Micrelenchus tenebrosus* and *Diloma subrostrata* (Fig. 2.2).

2.4.2 Seasonal survey: effects of seaweed species identity and biomass across seasons

Invertebrate abundance. The most abundant species were *Micrelenchus tenebrosus* (1,613 individuals), amphipods (1,037), *Diloma subrostrata* (405) and *Halicarcinus whitei* (191).

There were no significant interactions, and the only single factor effects were Species (Table 2.1, $p = 0.001$, η^2 = 9.2%) and Biomass ($p < 0.05$, η^2 = 3.4%), demonstrating that more invertebrates were associated with *Ulva* compared to *Gracilaria* (39.10 ± 3.05 ind. gDW seaweed^{-1} vs 21.83 ± 2.88) and with seaweeds with low than high biomass (39.85 ± 3.68 vs 25.05 ± 2.37) (Fig. 2.3A-B).

Invertebrate richness. There were four significant interactions, where the Species × Season interaction explained most of the data variability (Table 2.1, η^2 = 3%). Specifically, I found a significant interaction between the three key factors targeted in my main hypothesis (Species × Biomass × Season, $p < 0.05$, η^2 = 1.4%). This interaction showed that (i) *Ulva* supported more taxa than *Gracilaria* in summer, irrespective of the biomass, (ii) seaweeds with low biomass were inhabited by more taxa than seaweeds with large biomass, irrespective of the species identity and season, and that (iii) *Ulva* was inhabited by more taxa in summer than in winter, irrespective of the biomass (Fig. 2.3C-D). Season was not significant as a single factor, but interacted with the seaweed Species ($p < 0.01$, η^2 = 3%) and Elevation ($p < 0.05$, η^2 = 2%). Similarly, Biomass interacted with Elevation ($p < 0.05$, η^2 = 1.5%), showing that more taxa

were associated with seaweeds in low biomass from the intertidal zone. Among the single test factors, most data variability was explained by Biomass ($p = 0.001$, $\eta^2 < 25\%$), where more taxa were associated with seaweeds with low biomass (Fig. 2.3C-D). Furthermore, more taxa were associated with *Ulva* than *Gracilaria* and in the intertidal than the subtidal zones ($p < 0.05$).

Invertebrate community structure. There were four significant interactions (Table 2.1). Biomass interacted with Season ($p < 0.01$, $\eta^2 = 1.8\%$) and Species interacted with Elevation ($p < 0.01$, $\eta^2 = 1.7\%$) and Season ($p < 0.05$, $\eta^2 = 1.2\%$). Post-hoc t-test showed that communities differed between summer and winter for *Ulva* samples, and between *Ulva* and *Gracilaria* samples in the summer season. All single factors were significant, where most variability was explained by Biomass ($\eta^2 = 4.5\%$), followed by Elevation ($\eta^2 = 3.3\%$), Species ($\eta^2 = 2.3\%$) and Season ($\eta^2 = 1.6\%$) (Fig. 2.4). The MDS plot showed that *Ulva* samples were more dispersed than *Gracilaria* samples. Four taxa accounted for 50% of the data variability in the MDS plot (*Micrelenchus tenebrosus, Diloma subrostrata*, amphipods and *Halicarcinus whitei*), all correlated positively with the presence of *Ulva* (Fig. 2.4).

2.4.3 Experiment 1: effects of seaweed species identity and biomass across seasons

Invertebrate abundance. As in the spatial survey, amphipods (1,259 individuals), *Micrelenchus tenebrosus* (1,180) and *Diloma subrostrata* (846) dominated in the samples.

There were four significant interactions (Table 2.1). Species and Biomass interacted significantly with Elevation and Site ($p < 0.05$) but these interactions explained only little of the data variability. The Biomass × Season interaction explained most of the data variability ($\eta^2 = 6.5\%$). Seaweeds with medium and high biomass were inhabited by more invertebrates than seaweeds with low biomass but only in winter (Fig. 2.5B). The most important significant single factor effects were Season ($\eta^2 = 10\%$), followed by Elevation ($\eta^2 = 3\%$), showing that more invertebrates were found in summer than in winter and in the subtidal than intertidal elevation level (Fig. 2.5A-B).

Invertebrate richness. There were three significant interactions (Table 2.1), where Biomass × Season explained most of the data variability ($\eta^2 = 7.6\%$), showing more taxa associated with low seaweed biomass compared to large biomass in summer but not winter (Fig. 2.5C). All single factors, except Species, were significant. Season explained most of the data variability

($p = 0.001$, $\eta^2 = 12\%$), with two times more taxa being associated with seaweed in summer than winter (Fig. 2.5C-D). In addition, more taxa were found on low than medium or large seaweed biomass (Fig. 2.5C-D), in the subtidal than intertidal zone and at the site closest to the river mouth.

Invertebrate community structure. I found 11 significant interactions (Table 2.1). Biomass × Season explained most of the data variability ($\eta^2 = 4.5\%$) and pair-wise t-tests showed significant communities between all test factor combinations (Fig. 2.6). All the single test factors were also significant, and Season ($\eta^2 = 7\%$) and Biomass ($\eta^2 = 5\%$) explained most of the data variability. The MDS plot showed a separation of *Ulva* and *Gracilaria* samples, a pattern that was more distinct in summer than winter (Fig. 2.6A). Fifty percent of the multivariate community structure was explained by 5 taxa, where *Micrelenchus tenebrosus* and *Diloma subrostrata* were correlated with the presence of *Ulva*, whereas amphipods, copepods and juvenile crabs were correlated more with the presence of *Gracilaria* (Fig. 2.6).

2.4.4 Experiment 2: effects of structure vs being alive

Invertebrate abundance. Amphipods (380 individuals), *Micrelenchus tenebrosus* (341) and *Diloma subrostrata* (104) were again the dominant taxa.

Seaweed type was the only significant factor ($p = 0.001$, Table 2.1), explaining > 70% of data variability showing almost 10× more invertebrates in the living seaweeds compared to the mimics (Fig. 2.7A-C).

Invertebrate richness. Richness was affected by two significant interactions (Table 2.1). The highest 3-factor interaction ($\eta^2 = 7.8\%$) showed that living *Gracilaria* supported more taxa than the *Gracilaria* mimic when attached on *Austrovenus* mimics, a result further supported by the Type × Host interaction ($\eta^2 = 15\%$) (Fig. 2.7D-F). In addition, the number of taxa associated with living seaweeds attached to *Austrovenus* mimics was significantly higher compared to living seaweeds attached to living and dead cockle shells (Fig. 2.7D-F). Of the single test factors, Seaweed ($\eta^2 = 20\%$) and Host type ($\eta^2 = 20\%$) were significant, showing more invertebrates associated with *Gracilaria* compared to *Ulva*, and on *Austrovenus* mimics compared to live *Austrovenus* and *Austrovenus* shells.

Invertebrate community structure. There were three significant interactions, including the highest 3-factor interaction (Table 2.1). Seaweed type interacted with both Seaweed species and Host type (both individually and simultaneously, i.e., in 2- and 3-factor interactions) and was the only significant single factor ($p = 0.001$, $\eta^2 = 29\%$, Fig. 2.8). The MDS ordination showed clear separation between living seaweeds and seaweed mimics (Fig. 2.8) and 50% of the multivariate data variability was explained by amphipods, *Micrelenchus tenebrosus* and *Diloma subrostrata*, correlating positively with living seaweeds.

2.4.5 Experiment 3: effects of predators

Only four snails (2.2%) were found 'crushed' in this experiment, showing that *Hemigrapsus* have little direct predation effect on *Micrelenchus.* Additionally, the habitat that snails were observed in was not affected by the predator (Fig. 2.9). However, in the cages with mud and *Ulva*, snails were more often found attached to *Ulva* (59.5% and 73.6% with or without crabs, respectively; Fig. 2.9, $p < 0.001$, Appendix 2.6) than mud, whereas in cages with mud and *Gracilaria*, snails were more common on the mud (26.3% and 38.0% with or without crabs, respectively) than on the seaweed (Fig. 2.9, $p < 0.001$).

2.4.6 Habitat-affinity and correlations across surveys and experiments

Across data collections, samples were dominated by amphipods (6,505 individuals counted in total), *Micrelenchus tenebrosus* (4,201), *Diloma subrostrata* (1,629), and the crab *Halicarcinus whitei* (731). The spatial survey showed that *Ulva* was inhabited by more trochids (12.48 ± 1.77 ind. gDW seaweed^{-1} vs 6.04 ± 0.80, Fig. 2.10A), amphipods and copepods (44.37 ± 7.16 vs 20.00 ± 3.48) compared to *Gracilaria,* whereas the crab *Halicarcinus* was much more abundant on *Gracilaria* (3.40 ± 0.67 vs 1.10 ± 0.28). These results were supported by the seasonal survey (Fig. 2.10B), whereas Experiment 1 documented more gastropods (other than trochids) and crabs (other than *Halicarcinus whitei*) associated with *Ulva* but still more *Halicarcinus* on *Gracilaria* (Fig. 2.10C). Finally, results from experiment 2 showed significant difference between living and mimic secondary habitat formers with larger abundances of trochids, amphipods and copepods, crabs and spider crabs on living seaweeds compared to mimic seaweeds (Fig. 2.10D).

Finally, I found strong positive correlations between both living seaweeds biomass and invertebrate abundance (*Gracilaria*: $r_{Spearman} = 0.69$, $p < 0.001$; *Ulva*: $r_{Spearman} = 0.71$, $p < 0.001$; Fig. 2.11A) and taxonomic richness (*Gracilaria*: $r_{Spearman} = 0.53$, $p < 0.001$; *Ulva*: $r_{Spearman} =$

0.52, $p < 0.001$; Fig. 2.11B) (but note that invertebrate data, in these analyses, were not standardized by seaweed biomass). Since the mimics had an extremely low biomass range and all of them were virtually identical, it was not possible to analyse these seaweeds (and I only had a sample size of 9).

2.4.7 Morphological traits of habitat formers

All morphological traits were significantly different between habitat-forming species ($p = 0.001$, Fig. 2.12-2.13). Pair-wise t-tests showed significant differences for all traits between live *Ulva* and *Gracilaria* ($p = 0.001$). Similarly, *Ulva* and *Gracilaria* mimics had significantly different traits (except for lacunarity, Fig. 2.13). Live *Gracilaria* and *Ulva* were also significantly different from their abiotic mimics in certain traits. *Ulva* and the *Ulva*-mimic had different surface area:dry weight ratios ($p = 0.001$) and fractal dimension ($p = 0.009$), whereas *Gracilaria* and *Gracilaria*-mimic were different across all traits ($p = 0.001$). Finally, live cockles were also different from their mimics ($p = 0.001$) and both seaweed species ($p = 0.001$) across all traits.

2.5 DISCUSSION

This study compared two estuarine habitat cascades, demonstrating how ecological and morphological features of biogenic secondary habitat-forming seaweeds modify invertebrate communities. In this system primary habitat-forming cockles live burrowed just below the sediment surface where the spatially limited and structurally simple shell provides space for settlement of sessile organisms such as canopy-forming seaweeds (Mouritsen and Poulin 2003) and a few small invertebrates (Thomsen et al. 2016a). Colonization of the shell by canopy-forming seaweeds, that are fundamentally different in form and functions compared to the shell host, will thereby add not only more habitat-space but also new ecological niches, for example, with new grazing opportunities (Thomas et al. 1998, Wernberg et al. 2010), novel habitats to escape predation (Johnston and Lipcius 2012, Wright et al. 2014), and buffering of abiotic stress during low tide (Davison and Pearson 1996, Garbary 2007). In estuarine systems, these shell-seaweed habitat cascades are therefore likely to be strong, compared to, for example, habitat cascades in forests and on rocky shores (where primary and secondary habitat formers typically are plants with relatively similar form-functional traits), and may even give rise to higher order habitat cascades with many hierarchical layers of co-existing habitat formers (Thomsen et al. 2016a).

2.5.1 Second habitat former species identity and biomass and invertebrate affinity

The two surveys supported the hypothesis that *Ulva* and *Gracilaria* are inhabited by different assemblages. However, in contrast to my expectation, *Ulva* was generally a better habitat, probably because it is easier to consume for herbivores (discussed in next section). Many other studies have also found different invertebrates associated with different seaweed species (Beck 1998, 2000, Chemello and Milazzo 2002, Colman 1940, Kostylev et al. 1997, Seed and O'Connor 1981, Taylor and Cole 1994), typically concluding that structurally complex seaweeds host more diverse invertebrate communities than simpler morphologies (Cardoso et al. 2004, Chemello and Milazzo 2002, Hauser et al. 2006, Hicks 1985, Hull 1997). My results support Gee and Warwick (1994a), who showed that invertebrate diversity increased with increasing fractal dimensions. However, my results do not support Whatley and Wall (1975), who found that seaweeds with large flat fronds would provide limited protection from desiccation and wave action. My results also contrast with Ba-Akdah (2016) who found more invertebrates associated with *Gracilaria* than *Ulva*. Additionally, low seaweed biomass hosted proportionally more inhabitants and taxa than large biomass. Initially, this contrasts with past studies (Byers et al. 2012, Colman 1940, Drouin et al. 2011, Edgar 1983, Gore et al. 1981, Gunnill 1982, 1983, Hagerman 1966, Kangas 1978, Nagle 1968, Thomsen et al. 2016a, Thomsen et al. 2013, Zavodnik 1967), but the contradiction is largely an artefact because, in contrast to past studies, I standardized abundances by seaweed biomass. Indeed, the correlation analysis on un-standardized data supported past studies, as I found strong positive correlations between seaweed biomass and invertebrate abundances and richness.

My results show that *Ulva* was inhabited by more trochids, amphipods and copepods, probably because they feed directly on its tissue as demonstrated in many other studies (Cruz-Rivera and Hay 2001, D'Antonio 1985, Grahame 1973, Hagerman 1966, Kamermans et al. 2002, McBane and Croker 1983, Pederson and Capuzzo 1984, Poore 1994, Watson and Norton 1987). In addition, it has been shown that sheet-forming seaweeds can, for some prey and predators, offer higher protection against predation compared to branched seaweeds, particularly for amphipods (Coull and Wells 1983, Holmlund et al. 1990). Nevertheless, the crab *Halicarcinus* generally preferred *Gracilaria*. I am not aware of other studies showing habitat preferences by *Halicarcinus,* but I suggest that the colour and branching pattern of *Gracilaria* provide efficient camouflage for 'clinging' slow-moving crabs. Other factors, not measured here, including physiological, biomechanical and chemical attributes of the seaweed may also explain different host affinities (Bates 2009, Dawes et al. 2000, Steinberg et al. 1998).

2.5.2 Latitude and season

As expected, latitude had a strong effect on all response variables, but with different results for the two seaweed species, where *Ulva* was inhabited by more invertebrates in the central and southern regions whereas *Gracilaria* hosted more taxa in northern locations. It has been demonstrated that latitudinal gradients affect invertebrates (Hutchins 1947) and that, at higher latitudes, invertebrates need to adapt to less stable climate compared to lower latitudes (Dobzhansky 1950). Under these conditions, *Ulva* can represent a suitable habitat with its flat fronds, perhaps stabilizing cold weather better than *Gracilaria*, which structure is less suitable to shelter from wind and low temperatures (Siciliano et al., unpubl. data). On the other hand, *Gracilaria* may be inhabited by more invertebrates at northern latitudes (as I originally hypothesized) because of a general higher invertebrate diversity, warmer climate and stronger intertidal desiccation stress (Fischer 1960, MacArthur 1965, 1972, Spight 1976, Wallace 1878). Nevertheless, it is not clear why I found latitudinal differences in taxonomic richness for *Gracilaria* but not for *Ulva*.

Similarly, seasonal effects were also strong with higher abundances and more taxa found in summer, probably because buffering of temperature and desiccation stress is more important under warm conditions (Johnson and Scheibling 1987). These results support previous observation by Ba-Akdah et al. (2016), who also found more invertebrates associated with *Ulva* and *Gracilaria* during summer. Seasonal fluctuation in the invertebrate assemblages in intertidal habitats are well documented (Gunnill 1983, Johnson and Scheibling 1987) and are typically related to environmental conditions such as temperature and desiccation stress (Colman 1940, Gunnill 1983, Hagerman 1966), physiological features of seaweeds (Gunnill 1983, Hagerman 1966, Mukai 1971, Trotter and Webster 1984), and species interactions such as predation and competition (Edgar 1983, Hagerman 1966, Hicks 1977, 1980). Temperature and desiccation stress may be particularly important for small organisms that lack structures to limit water loss such as amphipods (the most abundant invertebrates in my study) which may therefore inhabit seaweeds during low tide (McBane and Croker 1983).

2.5.3 Types of habitat formers

My experiments showed that living seaweeds generally are a better habitat for invertebrates than seaweed mimics, regardless of their morphology, as all major taxonomic groups were more abundant on the living habitat formers. This is consistent with other studies that have shown higher epifaunal abundances on living rather than non-living seaweeds, suggesting that trophic subsidies to grazers is important in benthic systems (Bologna and Heck 1999, Boström

and Mattila 1999, Gartner et al. 2013, Viejo 1999). Still, structural effects are clearly also important because my transplanted mimics were all rapidly colonized by diverse invertebrate communities.

2.5.4 Predation experiment

There is evidence that *Micrelenchus dilatatus* is consumed by crabs in New Zealand (Ovalipes catharus, Wear and Haddon 1987). Nevertheless, I found almost no predation on *Micrelenchus* in the Avon-Heathcote, suggesting that this gastropod is unlikely to inhabit seaweeds to avoid predation. My predation experiments thereby contrast other studies, which found a lower predation rate in presence of seaweeds (Adams et al. 2004, Boström and Mattila 1999, Leber 1985), also for the congeneric seaweed *Ulva lactuca* (Wilson et al. 1990b).

2.5.5 Habitat cascades

The habitat cascades documented here appear to be relatively similar to other mollusc-seaweed (Albrecht and Reise 1994, Koivisto and Westerbom 2010, Thomsen et al. 2016a, Thomsen et al. 2010) or plant-mollusc (Altieri and Irving 2017, Altieri et al. 2007, Altieri et al. 2010, Angelini et al. 2015, Valentine and Heck Jr 1993) cascades. A common features of these cascades is the strong morphological difference between the primary and secondary habitat formers which, theoretically, should lead to stronger effects compared to cascades where habitat formers are ecologically similar (Angelini and Silliman 2014, Thomsen et al. 2016a, Thomsen et al. 2010). By contrast, cascades where primary and secondary habitat formers are both plants (Cruz-Angòn et al. 2009, Cruz-Angòn and Greenberg 2005, Koh 2008, Watson 2002) or seaweeds (Buzá-Jacobucci and Pereira-Leite 2014, Thomsen et al. 2016b, Viejo and Åberg 2003, Worm and Sommer 2000) are less different and, consequently, indirect facilitations appear to be less strong.

2.5.6 Conclusions

Seaweed-invertebrate interactions can be strongly affected by several seaweed attributes (Wernberg et al. 2013) not considered in this study such as chemistry and palatability to grazers (Haavisto et al. 2001, Hemmi and Jormalainen 2002, Kraufvelin et al. 2006, Orav-Kotta and Kotta 2004) or the colour, texture and morphology if used for shelter (Hacker and Madin 1991, Orav-Kotta and Kotta 2004, Thomsen et al. 2010). In addition, structural complexity and inhabitants' habitat perception are strongly scale-dependent (Dibble et al. 2006, Hansen et al.

2011). My study should be supplemented with direct tests of how seaweed attributes affect host affinities, and test how affinities may be modified by habitat complexity and scale.

This study reported a strong positive effect of secondary habitat-forming seaweeds attached to cockles in sedimentary estuaries, where *Ulva* was a better habitat than *Gracilaria*, probably reducing temperature fluctuations and desiccation stress and providing food resources for grazers. Thereby, these habitat-forming seaweeds fundamentally change the invertebrate assemblages found in sedimentary estuaries.

Tables

Table 2.1 Overview of PERMANOVA reporting the results of the factorial analysis. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Values represent the contribution of each test factor to the total data variability of the PERMANOVA models ($\eta^2 = SS_{Explained}/SS_{Total}$). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. See Appendix 3-2.2, 3-2.3, 3-2.4 and 3-2.5 for complete PERMANOVA tables. Significant values are in bold (*: p = 0.05-0.01, **: p = 0.01-0.001, ***: p < 0.001).

Factors	Abundance	Richness	Community structure
Spatial survey: effects of seaweed species identity and biomass across latitudes			
Seaweed species (Spe)	**4.83%*** **	**4.38%*** **	**1.87%*** **
Seaweed biomass (Bio)	0.67%	**24.34%*** **	**3.51%*** **
Elevation (Ele)	**4.06%*** **	0.08%	**2.37%*** **
Latitude (Lat)	0.51%	**2.59%** **	**6.92%*** **
Estuary(Latitude) (Est(Lat))	**11.69%*** **	**6.83%*** **	**26.23%*** **
Spe × Bio	0.75%	**1.02%***	0.29%
Spe × Ele	0.07%	0.09%	**0.37%***
Spe × Lat	**2.40%** **	**2.99%** **	**0.89%** **
Bio × Ele	0.11%	0.06%	0.27%
Bio × Lat	1.00%	1.06%	**1.15%*** **
Ele × Lat	0.87%	0.09%	**1.83%*** **
Spe × Est(Lat)	**4.74%** **	2.53%	**6.67%*** **
Bio × Est(Lat)	3.05%	**4.59%***	**3.01%** **
Ele × Est(Lat)	**9.09%*** **	**5.58%*** **	**4.82%*** **
Spe × Bio × Ele	**1.02%***	0.02%	0.28%
Spe × Bio × Lat	0.43%	0.94%	0.53%
Spe × Ele × Lat	**2.16%** **	0.35%	**0.72%***
Bio × Ele × Lat	**1.59%***	0.57%	**0.83%** **
Spe × Bio × Est(Lat)	**5.06%***	2.71%	**2.61%*** **
Spe × Ele × Est(Lat)	**3.03%***	**2.36%***	**1.32%***
Bio × Ele × Est(Lat)	1.34%	1.19%	1.32%
Spe × Bio × Ele × Lat	0.89%	0.03%	0.30%
Spe × Bio × Ele × Est(Lat)	0.61%	**1.52%***	0.41%
Seasonal survey: effects of seaweed species identity and biomass across seasons			
Seaweed species (Spe)	**9.21%*** **	**3.25%** **	**2.34%*** **
Seaweed biomass (Bio)	**3.42%***	**24.20%*** **	**4.49%*** **
Elevation (Ele)	0.16%	1.57%*	**3.31%*** **
Season (Sea)	0.00%	0.72%	**1.61%** **
Spe × Bio	0.03%	0.53%	0.69%
Spe × Ele	0.74%	0.11%	**1.72%** **
Spe × Sea	0.37%	**2.91%** **	**1.16%***
Bio × Ele	0.54%	**1.67%***	0.44%
Bio × Sea	0.05%	0.03%	**1.83%** **
Ele × Sea	0.98%	**1.86%***	0.72%

Spe × Bio × Ele	0.95%	0.01%	0.30%
Spe × Bio × Sea	0.65%	**1.36%***	0.41%
Spe × Ele × Sea	0.02%	0.16%	**1.32%***
Bio × Ele × Sea	0.88%	0.61%	0.48%
Spe × Bio × Ele × Sea	1.54%	1.21%	0.63%
Experiment 1: effects of seaweed species identity and biomass across seasons			
Seaweed species (Spe)	0.22%	1.08%	**1.39%****
Seaweed biomass (Bio)	0.55%	**2.66%***	**5.15%*****
Elevation (Ele)	**3.24%****	**3.82%****	**2.20%*****
Site (Si)	0.56%	**1.80%***	**1.35%****
Season (Sea)	**10.34%*****	**12.05%*****	**7.06%*****
Spe × Bio	0.00%	0.07%	0.87%
Spe × Ele	0.93%	0.85%	**0.88%****
Spe × Si	0.37%	1.23%	0.14%
Spe × Sea	0.02%	0.21%	0.22%
Bio × Ele	2.07%	1.08%	**1.27%***
Bio × Si	1.57%	1.31%	**1.36%****
Bio × Sea	**6.50%****	**7.57%****	**4.47%*****
Ele × Si	0.24%	0.01%	**2.14%*****
Ele × Sea	1.13%	**2.01%***	**0.80%****
Si × Sea	0.13%	0.65%	0.38%
Spe × Bio × Ele	0.89%	0.80%	0.82%
Spe × Bio × Si	**2.66%***	1.53%	**2.11%*****
Spe × Bio × Sea	0.17%	0.17%	0.63%
Spe × Ele × Si	**1.84%***	**2.22%****	**0.87%****
Spe × Ele × Sea	1.36%	1.11%	**0.82%***
Spe × Si × Sea	0.00%	0.03%	0.16%
Bio × Ele × Si	0.70%	0.93%	0.53%
Bio × Ele × Sea	0.36%	0.23%	0.37%
Bio × Si × Sea	1.36%	0.48%	**1.61%*****
Ele × Si × Sea	0.12%	0.04%	0.65%*
Spe × Bio × Ele × Si	**2.29%***	1.81%	0.38%
Spe × Bio × Ele × Sea	0.73%	0.51%	0.51%
Spe × Bio × Si × Sea	0.32%	0.71%	**0.94%***
Spe × Ele × Si × Sea	0.47%	0.19%	0.34%
Bio × Ele × Si × Sea	0.12%	0.21%	**0.99%***
Spe × Bio × Ele × Si × Sea	0.05%	0.28%	0.02%
Experiment 2: effect of structure vs being alive			
Seaweed species (Spe)	0.07%	3.34%	2.01%
Seaweed type (Typ)	**72.50%*****	**38.87%*****	**29.04%*****
Host type (Hos)	2.07%	**19.57%****	4.38%
Typ × Spe	1.69%	1.33%	**3.78%***
Typ × Hos	5.03%	**15.37%****	**7.30%***
Spe × Hos	1.16%	6.72%	5.04%
Typ × Spe × Hos	1.67%	**7.77%***	**8.37%****

Table 2.2 Averages of abundances of invertebrate taxa found associated with *Austrovenus stutchburyi* without epibiota (A) vs with attached *Gracilaria chilensis* (AG), *Ulva* sp. (AU), *Gracilaria* mimics (AGm), or *Ulva* mimics (AUm). The most common taxa attached to *Austrovenus* shells (with and without *Ulva* or *Gracilaria* attached) were the anemone *Anthopleura* sp. (81 individuals in total), the limpet *Notoacmea helmsi* (40) and the barnacle *Chamaesipho columna* (37).

	n	Snails	Amphipods, copepods, isopods	Crabs	Polychaetes	Sea anemone	Bivalves	Other
A	115	0.30	0.02	0.00	1.15	0.09	0.01	0.00
AG	287	7.17	10.53	1.75	2.70	0.25	0.31	0.05
AU	256	9.37	9.47	0.97	2.62	0.33	0.11	0.05
AGm	9	7.00	5.78	1.33	2.78	0.11	0.00	0.00
AUm	9	5.00	1.33	0.44	0.22	0.00	0.11	0.11

Figures

Figure 2.1 Spatial survey, effects of seaweed species identity and biomass across latitudes. Abundance (A, B, C) and richness (D, E, F) of invertebrates associated with *Gracilaria chilensis* (G, dark grey) or *Ulva* sp. (U, grey) at low (L) and high (H) biomass from northern (A, D), central (B, E) and southern (C, F) latitudes. Collected seaweed were attached to the cockle *Austrovenus stutchburyi.* Results from *Austrovenus* collected without attached seaweed were not shown because very few invertebrates inhabited the shells (Table 2.2). Data were standardized by seaweed dry weight. Error bars = 1 SE. n = 32. The test factors 'Estuaries' and 'Elevation' were pooled. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'Species' test factor, lower case letters to the 'Species × Biomass' interaction.

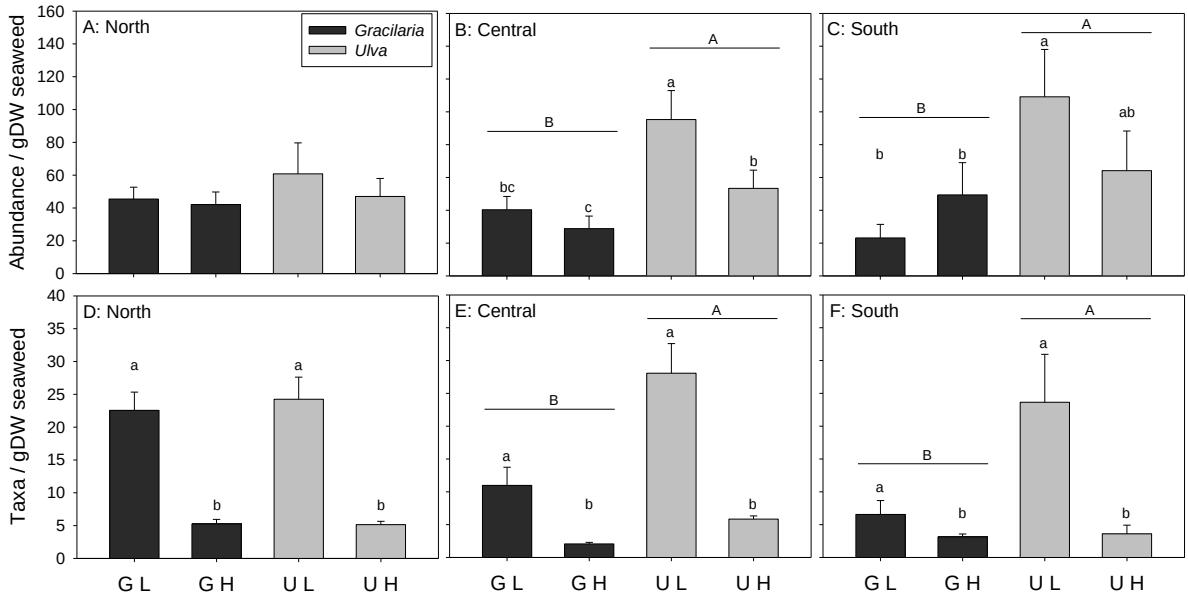


Figure 2.2 Spatial survey, effects of seaweed species identity and biomass across latitudes. MDS plot of community structure (based on the Bray-Curtis similarity coefficient) for *Gracilaria chilensis* (dark grey), *Ulva* sp. (grey) in low (circle) and high (square) biomass from northern (A), central (B) and southern latitudes (C). Results from *Austrovenus stutchburyi* collected without attached seaweed were not shown because very few invertebrates inhabited these shells (Table 2.2). For simplicity, data were split into northern, central and southern latitudes but results are from the same analysis and the three plots can be superimposed on each other (and therefore have the same taxa vectors). Data were standardized by seaweed dry weight and square-root transformed. n = 32. The test factors 'Estuary' and 'Elevation' were pooled. A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: amphipods, 2: *Micrelenchus tenebrosus*, 3: *Diloma subrostrata*). Stress: 0.22.

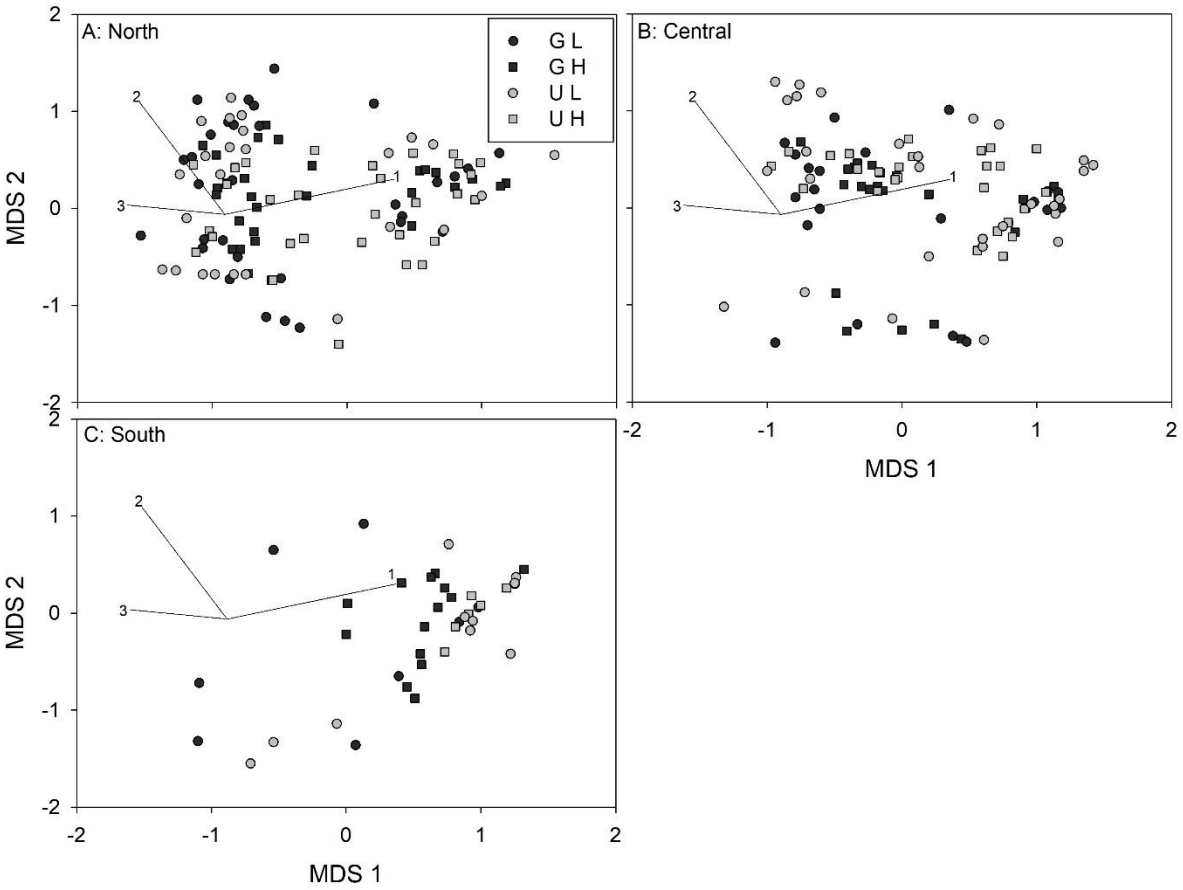


Figure 2.3 Seasonal survey, effects of seaweed species identity and biomass across seasons. Abundance (A, B) and richness (C, D) of invertebrates associated with *Gracilaria chilensis* (black) and *Ulva* sp. (grey) in high (H) and low (L) biomass in summer (A, C) and winter (B, D). Results from collected *Austrovenus stutchburyi* without attached seaweed were not shown because few invertebrates inhabited shells (Table 2.2). Data were standardized by dry weight of the secondary habitat former. Error bars = 1 SE, n = 24. The test factor 'Elevation' was pooled. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'Species' test factor, lower case letters to the 'Biomass' test factor.

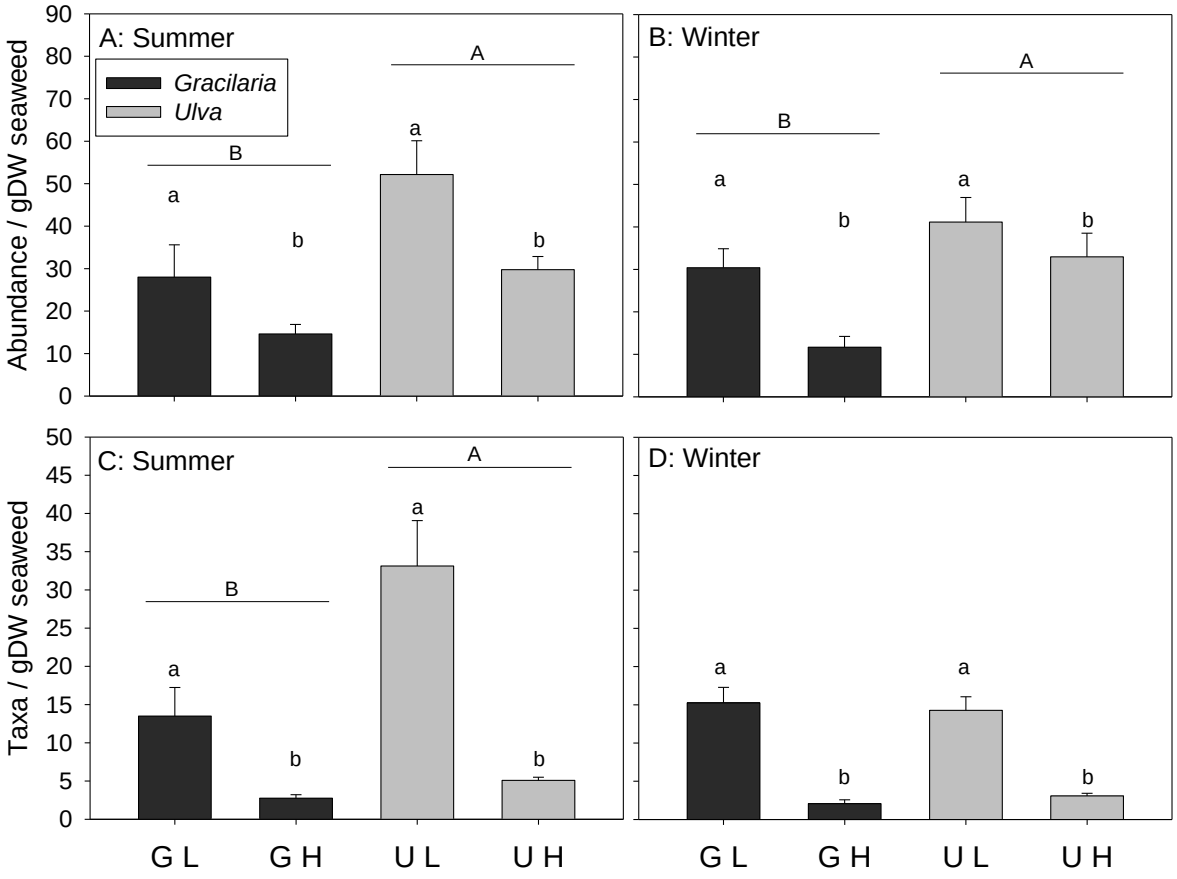


Figure 2.4 Seasonal survey, effects of seaweed species identity and biomass across seasons. MDS based on community structure (based on Bray-Curtis similarity coefficient) for *Gracilaria chilensis* (black) and *Ulva* sp. (grey) in low (circle) and high (square) biomass, in summer (A) and winter (B). Results from collected *Austrovenus stutchburyi* without attached seaweed were not shown because very few invertebrates inhabited these shells (Table 2.2). For simplicity, data were split into summer and winter but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). Data were standardized by dry weight of the seaweed and square-root transformed. n = 24. The test factor 'Elevation' was pooled. A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: *Micrelenchus tenebrosus*, 2: amphipods, 3: *Diloma subrostrata*, 4: *Halicarcinus whitei*). Stress: 0.24.

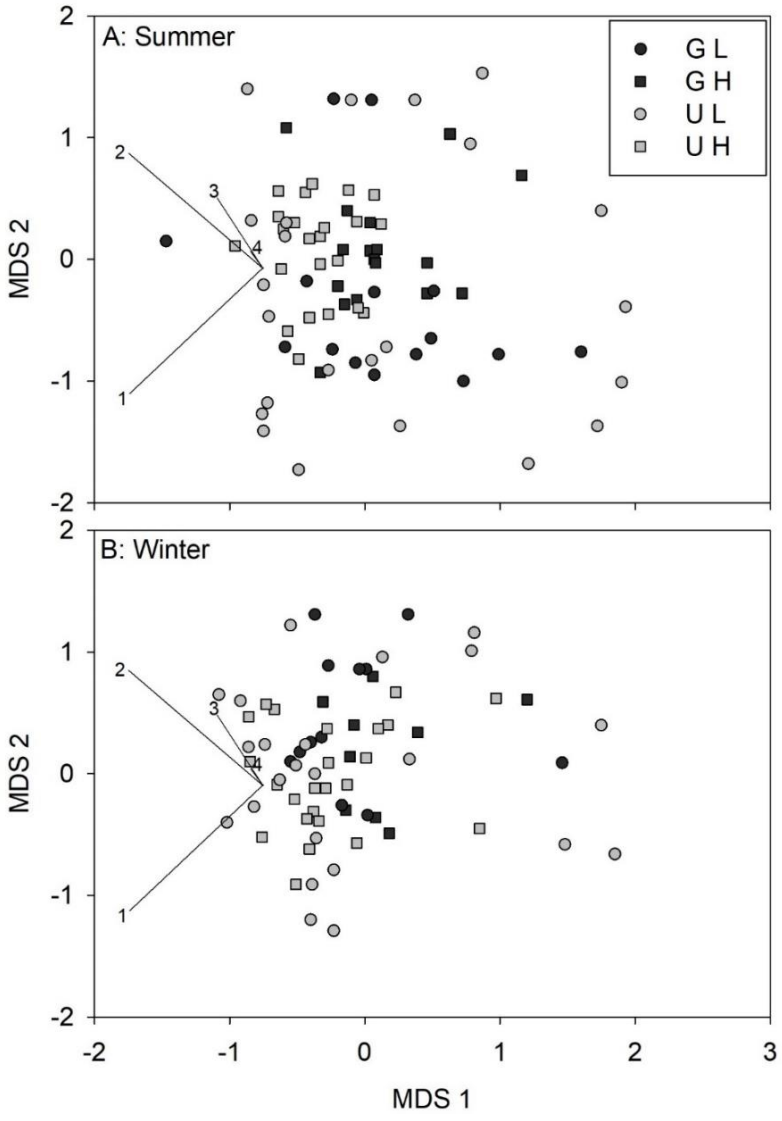


Figure 2.5 Field experiment 1, effects of seaweed species identity and biomass across seasons. Abundance (A, B) and richness (C, D) of invertebrates inhabiting *Gracilaria chilensis* (black) and *Ulva* sp. (grey) in low (L), medium (M) and high (H) biomass in summer (A, C) and winter (B, D). Data were standardized by dry weight seaweed. Error bars = 1 SE, n = 20. The test factors 'Site' and 'Elevation' were pooled. Different letters indicate significant differences for the significant 'Species × Biomass' interaction.

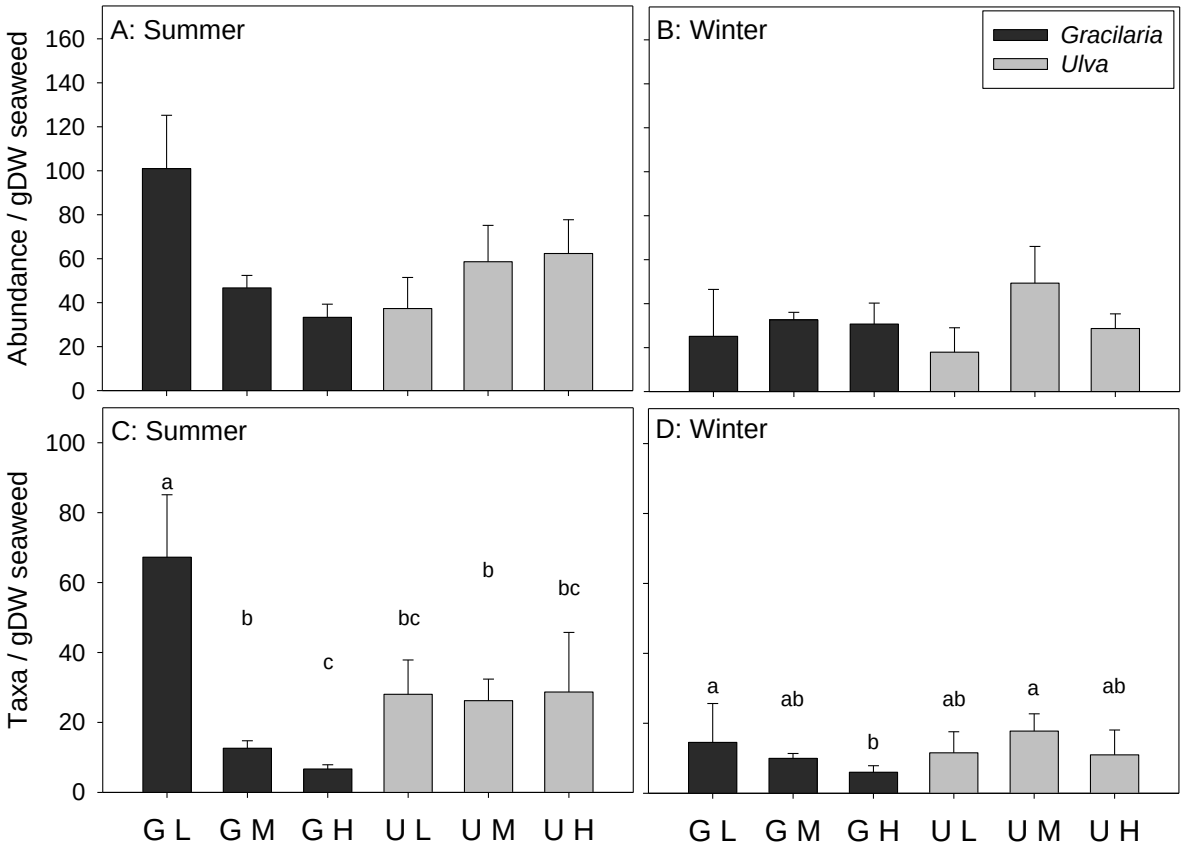


Figure 2.6 Field experiment 1, effects of seaweed species identity and biomass across seasons. MDS based on community structure (based on Bray-Curtis similarity coefficient) for *Gracilaria chilensis* (black) and *Ulva* sp. (grey) in low (triangle down), medium (circle) and high (triangle up) biomass in summer (A) and winter (B). For simplicity, data were split into summer and winter but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). Data were standardized by dry weight seaweed and square-root transformed. The test factors 'Site' and 'Elevation' were pooled. n = 20. A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: *Micrelenchus tenebrosus*, 2: *Diloma subrostrata*, 3: amphipods, 4: copepods, 5: juvenile crabs). Stress: 0.19.

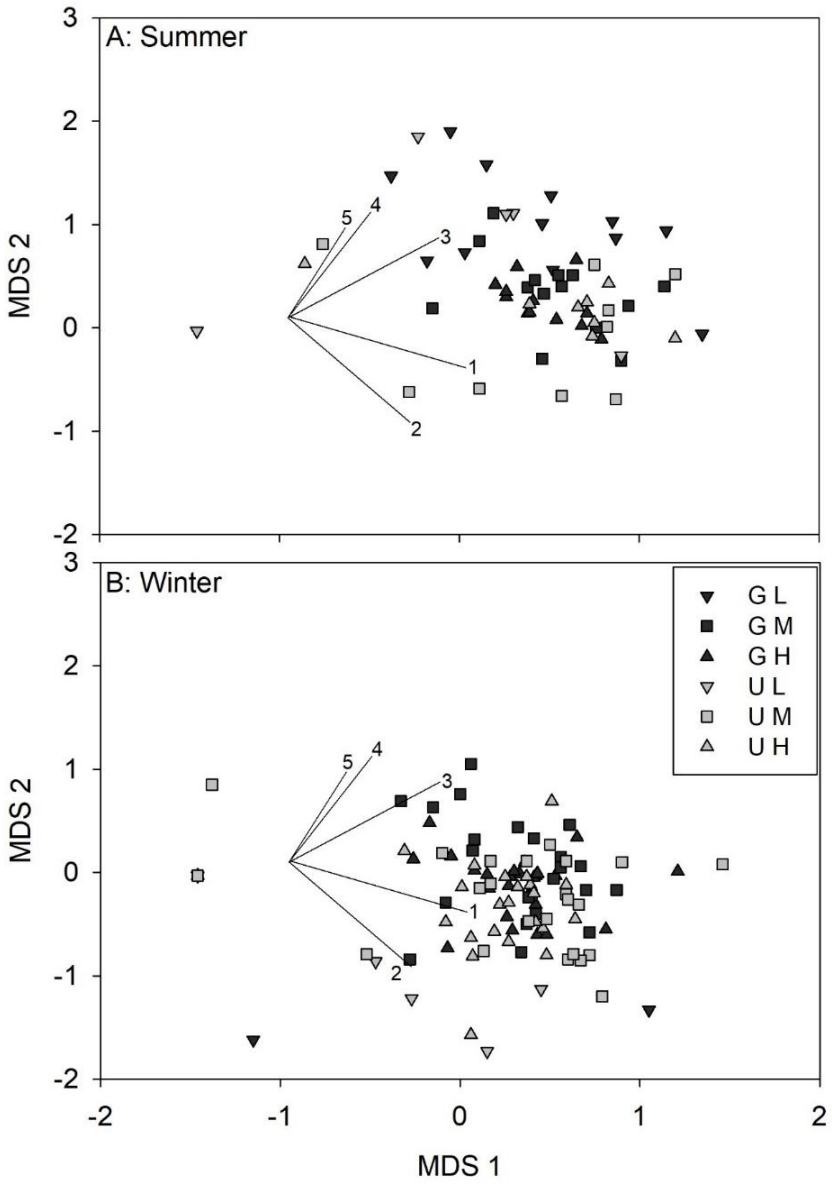


Figure 2.7 Field experiment 2, effects of structure vs being alive. Abundance (A, B, C) and richness (D, E, F) of invertebrates in *Gracilaria chilensis* (G) and its mimic (Gm), and *Ulva* sp. (U) and its mimic (Um) attached to live *Austrovenus stutchburyi* (A, D), to *Austrovenus* mimics (B, E) or to *Austrovenus* shells (C, F). Results from *Austrovenus* collected without attached seaweed were not shown because very few invertebrates inhabited these shells (Table 2.2). Data were standardized by seaweed dry weight. Error bars = 1 SE, n = 3. Different letters indicate significant differences. Capital letters refers to the 'Species' test factor, lower case letters to the 'Biomass' test factor.

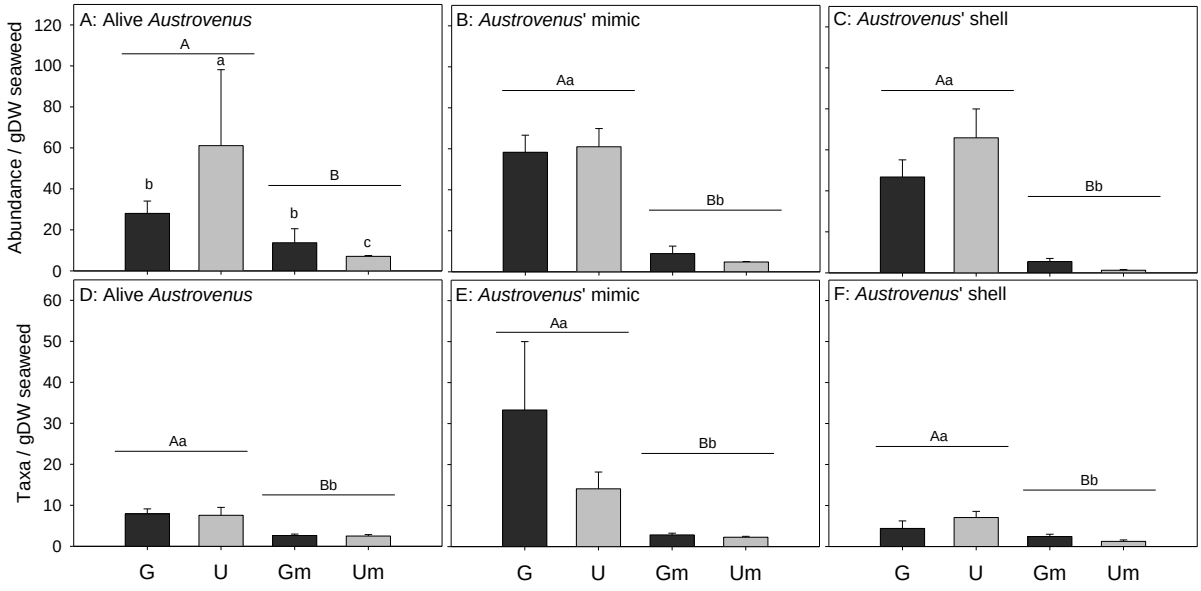


Figure 2.8 Field experiment 2, effects of structure vs being alive. MDS based on community structure (based on Bray-Curtis similarity coefficient) for living and mimics (m) of *Gracilaria chilensis* (G) and *Ulva* sp. (U). Data were standardized by dry weight seaweed and square-root transformed prior to analysis. The test factor 'Host' was pooled. n = 9. Results from collected *Austrovenus stutchburyi* without attached seaweed were not shown because very few invertebrates inhabited these shells (Table 2.2). A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: amphipods, 2: *Micrelenchus tenebrosus*, 3: *Diloma subrostrata*). Stress: 0.16.

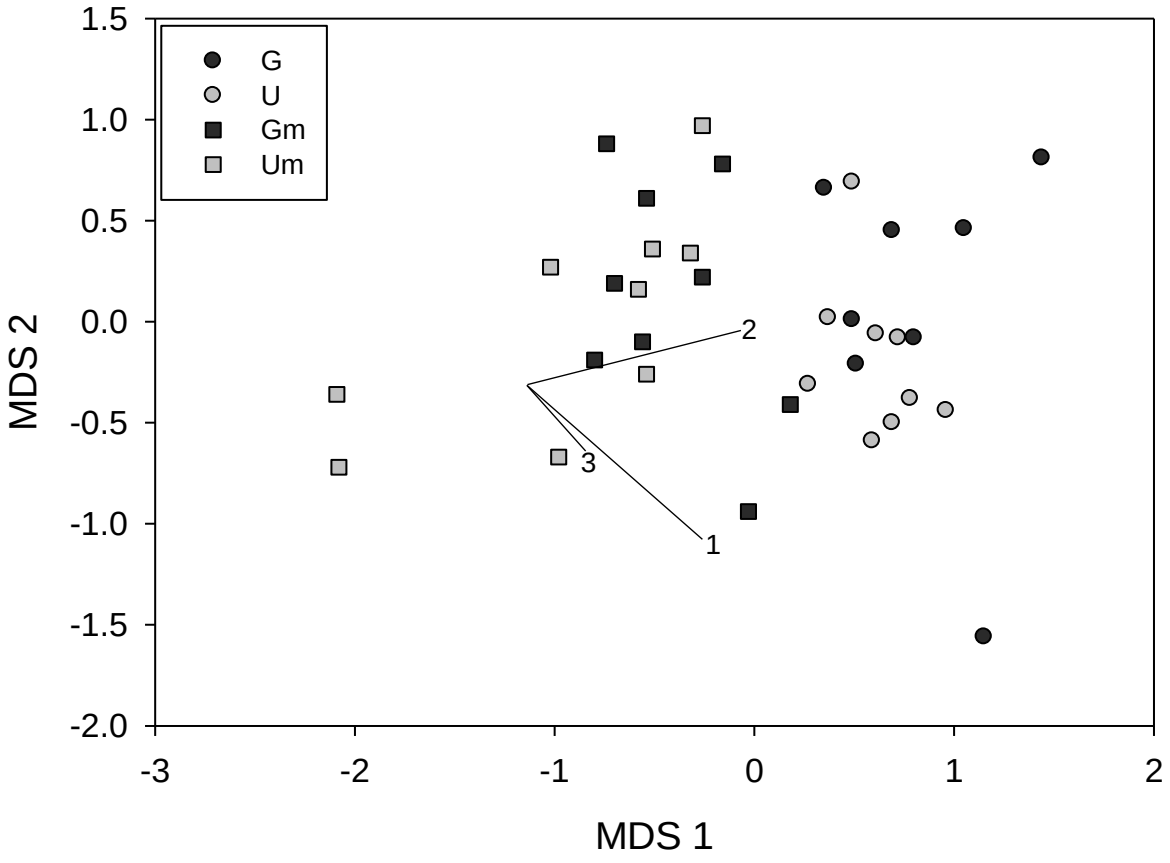


Figure 2.9 Field experiment 3, testing if the predatory crab *Hemigrapsus crenulatus* modifies habitat occupancy of the herbivorous gastropod *Micrelenchus tenebrosus*. +/-: presence/absence of predator. Only 2.2% of all gastropods exposed to predatory crabs were crushed. Gastropods were found inhabiting mud or attached to *Ulva* sp. or *Gracilaria chilensis*. The test factor 'Biomass' was pooled. n = 5.

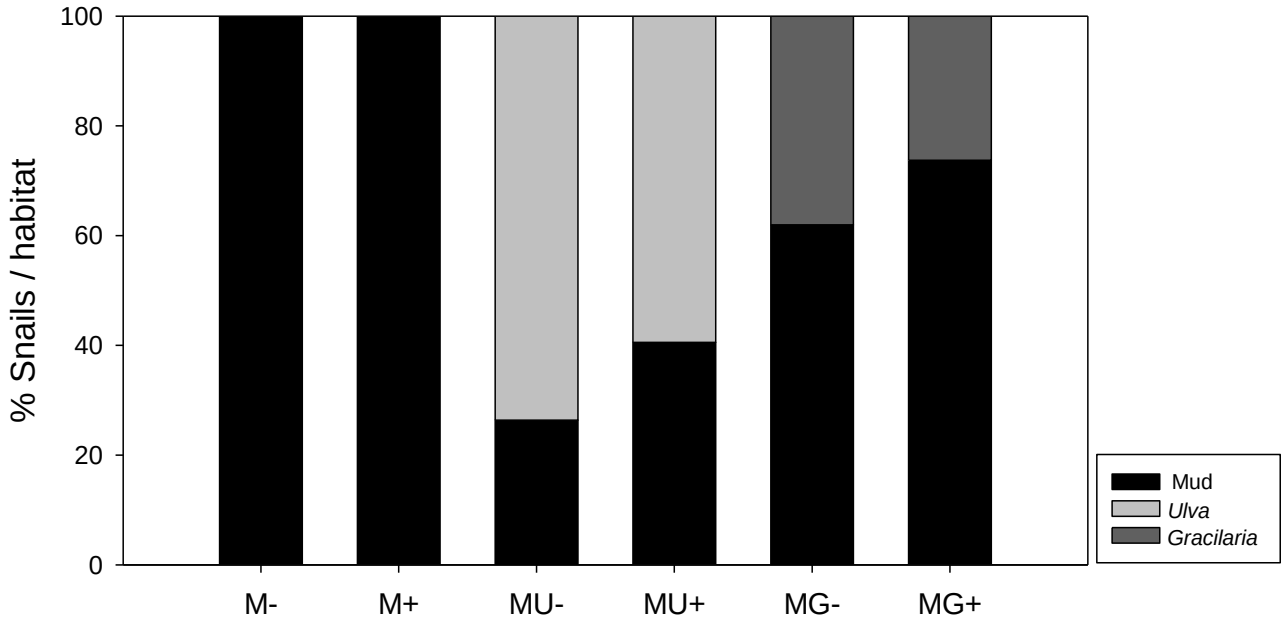


Figure 2.10 Host-affinity of invertebrates quantified from a spatial survey (A), a seasonal survey (B), and two field experiments (C-D). Hosts were either *Gracilaria chilensis* or *Ulva* sp. (plain pattern, black and grey respectively), *Gracilaria* mimic or *Ulva* mimic (both white but fine pattern with different orientation). Gastropods, excluding trochids, were mainly *Cellana* sp., *Notoacmea* sp., *Amphibola* sp., *Cominella* sp., trochids were *Diloma subrostrata* and *Micrelenchus tenebrosus*, crabs were *Hemigrapsus* sp., *Macrophthalmus* sp., *Austrohelice crassa*, and *Cyclograpsus lavauxi*, spider crabs were mainly *Halicarcinus whitei*, and 'others' were isopods, polychaetes, bivalves, chitons, and ostracods. Data were standardized by seaweed dry weight. Error bars = 1 SE, n = 9. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

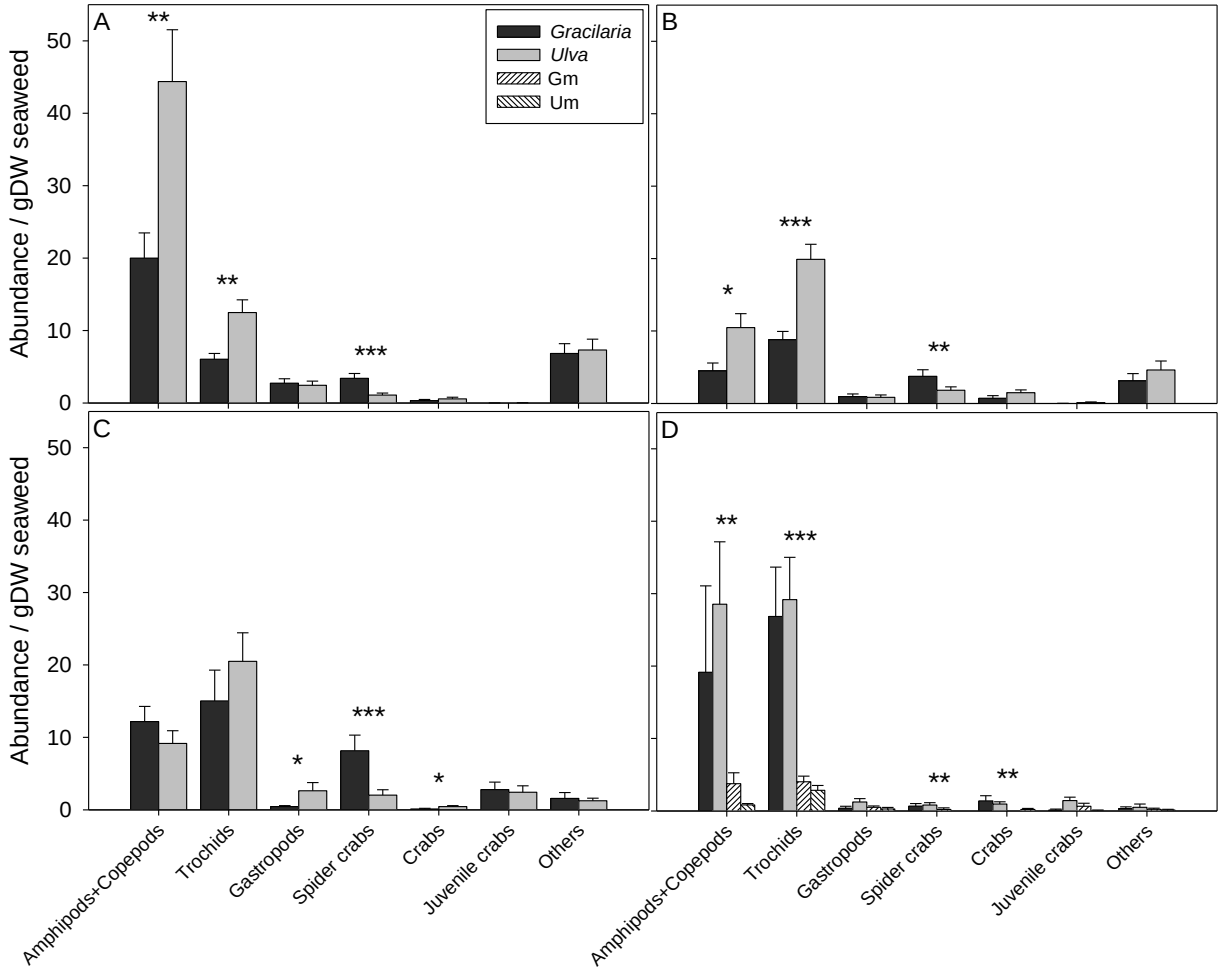


Figure 2.11 Correlation between the biomass of secondary habitat-forming seaweed (G: *Gracilaria chilensis*, U: *Ulva* sp., Gm: *Gracilaria* mimic, Um: *Ulva* mimic) and the abundance (A) and richness (B) of invertebrates. *Ulva*, n = 249; *Gracilaria*, n = 282; *Ulva* mimic, n = 9; *Gracilaria* mimic, n = 9.

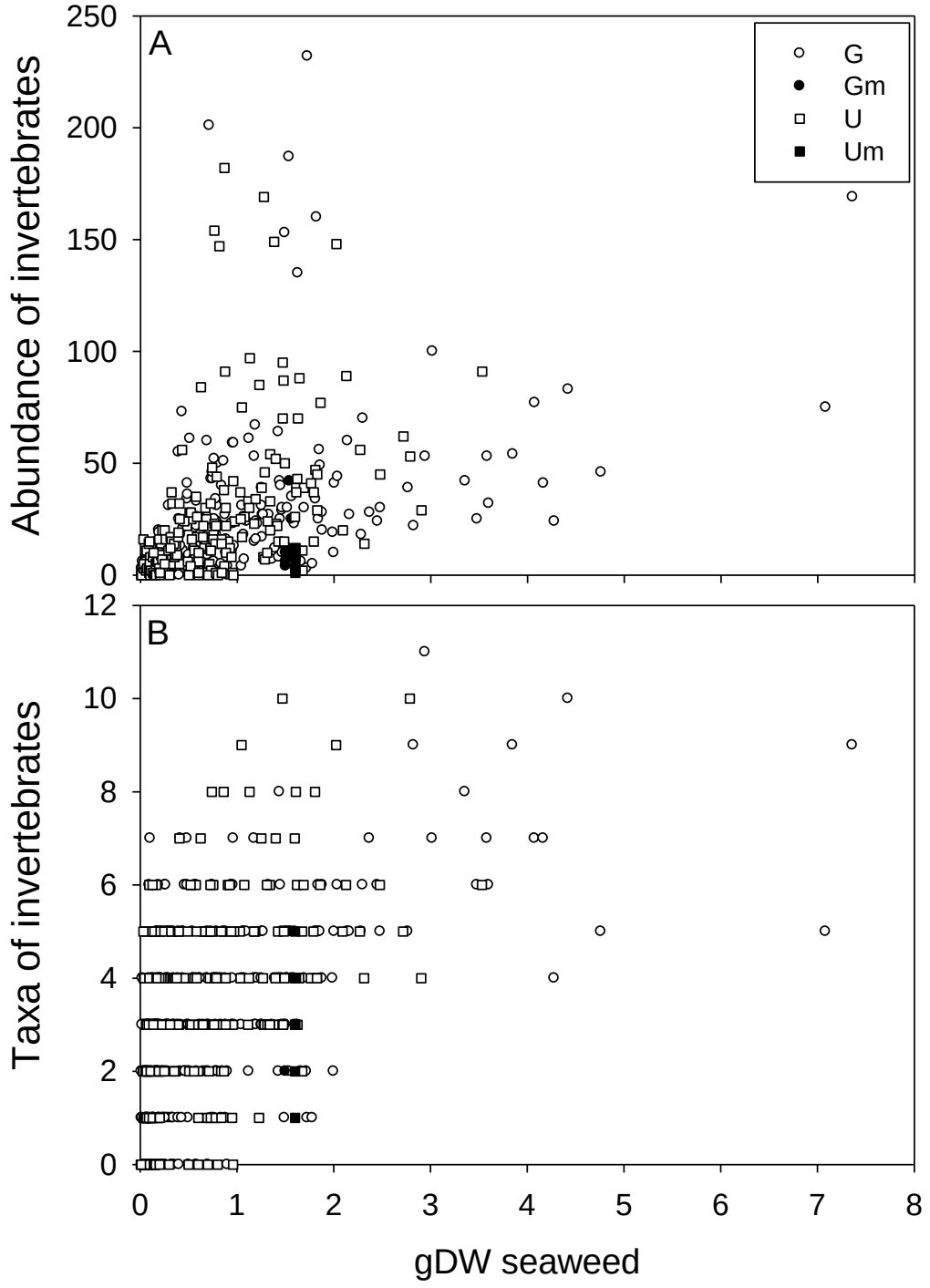


Figure 2.12 PCO analysis of morphological traits of living (circles) and non-living mimics (squares) primary habitat-forming cockles (white: *Austrovenus stutchburyi*, A) and secondary habitat-forming seaweeds (black: *Gracilaria chilensis*, G; grey: *Ulva* sp., U). n = 10. SDw: surface area:dry; Db: fractal dimension; C: circularity; Λ: lacunarity. Data were square-root transformed and normalised prior to analysis.

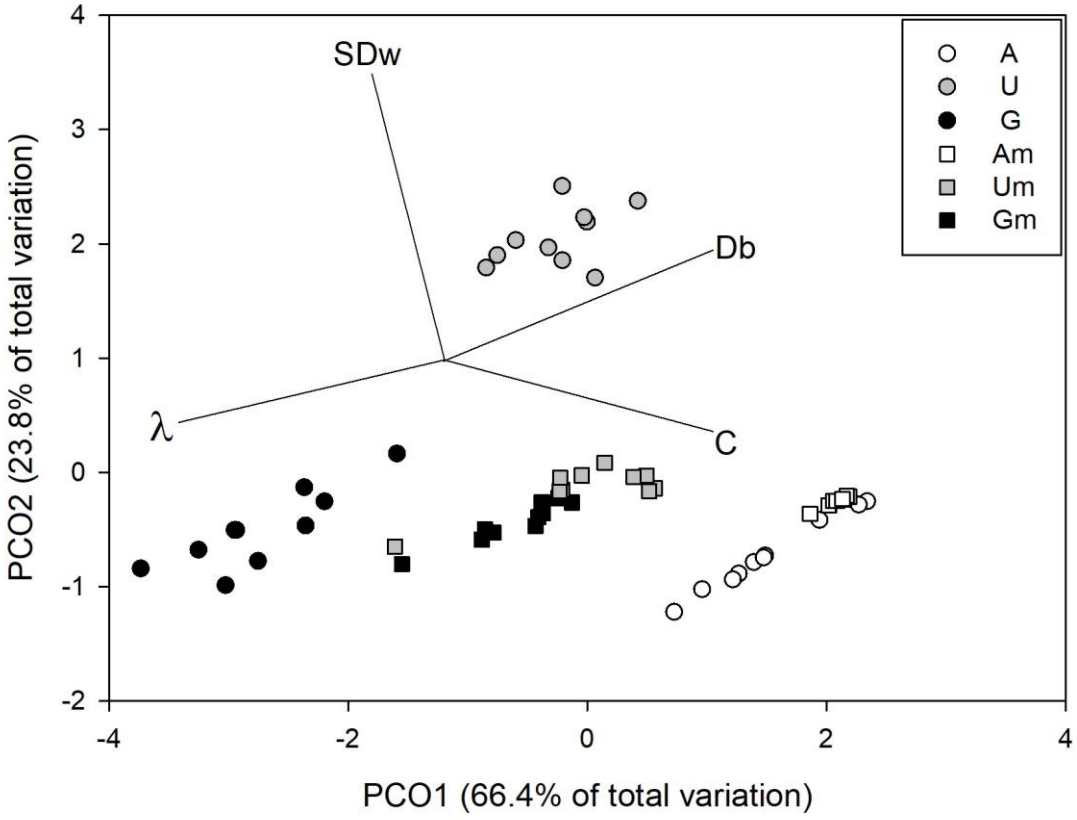
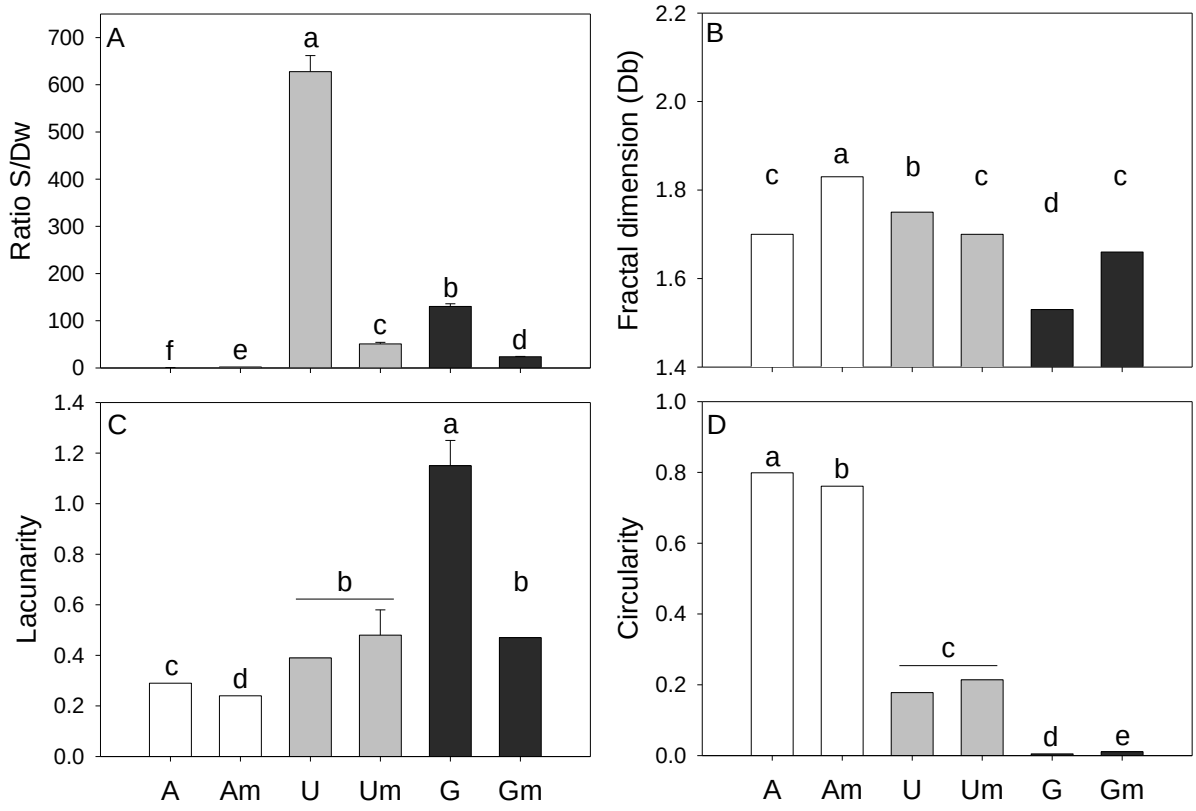


Figure 2.13 Morphological traits of primary habitat-forming cockles (A: *Austrovenus stutchburyi*, Am: *Austrovenus* mimic) and secondary habitat-forming seaweeds (U: *Ulva* sp., Um: *Ulva* mimic, G: *Gracilaria chilensis*, Gm: *Gracilaria* mimic). Error bars = 1 SE, n = 10. In most of cases, error bars are too small to be visible. Different letters indicate significant different treatments.



CHAPTER 3: Are long habitat formation cascades common? - A test with an estuarine 4-level interaction chain

3.1 ABSTRACT

Many studies have shown that two co-occurring habitat-forming species increase biodiversity compared to systems dominated by a single habitat-forming species. However, in some places, three or more habitat formers may co-occur, perhaps causing complicated effects on local communities. My aim is to document a new 'long habitat formation cascade' where the primary bivalve *Austrovenus stutchburyi* provides attachment space for the secondary seaweed *Gracilaria chilensis* that, again, provides substratum for the tertiary epiphytic seaweed *Ulva* sp. I tested if this long bivalve-seaweed-seaweed cascade affected invertebrate communities and if it is a general process operating across *Gracilaria* biomass, seasons, elevation levels, sites and estuaries. An observational study and a natural experiment confirmed that *Ulva* generally increased invertebrate abundances and altered community structures, whereas increases in taxonomic richness were only observed under a smaller subset of environmental conditions. These positive effects were, however, were not apparent in an experiment where I used non-living *Ulva* mimics, suggesting that common invertebrates graze on *Ulva*. Finally, analyses of all the data in a single quantitative synthesis confirmed that presence of epiphytic *Ulva* on *Gracilaria* significantly increased abundance of associated invertebrates whereas an observed net increase in richness was not statistically significant from zero. I also note that many results were variable between elevation levels, seasons, sites and estuaries, demonstrating that conclusions derived from single-site data collections should be interpreted cautiously. Based on these results and a growing number of observations from systems like marine benthic habitats where epibiosis is common, I suggest that many other long habitat cascades are likely to exist, and encourage more research into these processes to better understand how co-existing habitat-forming species affect local communities.

3.2 INTRODUCTION

Positive species interactions are ecologically important processes (Bertness and Callaway 1994, Bertness and Leonard 1997, Bruno et al. 2003, Callaway 1995, Stachowicz 2001) that occur through direct facilitation like mutualism, and habitat formation and modification, or indirect facilitation arising through processes like keystone predation, trophic cascades or facilitation and habitat formation cascades (Bishop et al. 2012, Borer et al. 2005, Cordero et al.

2012, Johnston and Lipcius 2012, Jones et al. 1997, Levine 1999, Menge 1995, Mouritsen 2004, Paine 1969, Thomsen et al. 2010, Yakovis et al. 2008). Of these indirect facilitation processes, habitat formation cascades (hereafter 'habitat cascades') mediated by sequential biogenic habitat formation (Thomsen et al. 2010) has received least research scrutiny. Nevertheless, these processes have been documented from freshwater (Blanco et al. 2008, Mormul et al. 2010, Shannon et al. 1994, Visconti et al. 2015), marine (Bologna and Heck 1999, 2000, Edgar and Robertson 1992, Martin-Smith 1993, Schneider and Mann 1991b, Thomsen 2010, Thomsen et al. 2016a, Thomsen et al. 2016b, Thomsen et al. 2010), saltmarsh and mangrove (Altieri et al. 2007, Altieri et al. 2010, Angelini et al. 2015, Bishop et al. 2012, Bishop et al. 2013, Bishop et al. 2009, Dijkstra et al. 2012, McAfee et al. 2016), and terrestrial (Angelini and Silliman 2014, Cruz-Angòn et al. 2009, Cruz-Angòn and Greenberg 2005, Díaz et al. 2012, Stuntz et al. 2003) ecosystems. Taken in concert, these studies suggest that habitat cascades can increase biodiversity across a variety of ecosystems, habitats and spatio-temporal scales.

Almost all these studies have quantified facilitation arising from 3-tiered interaction chains where 'primary' habitat formers provide habitat for 'secondary' habitat formers, that again provide habitat for habitat-using species (hereafter 'inhabitants'). Still, as shown for trophic cascades (Tronstad et al. 2010), analogue longer habitat cascades may exist, and perhaps with more complex effects on inhabitant communities. To date, I am aware of three studies, all from marine sedimentary systems, that have quantified positive effects on inhabitants arising from more than two co-occurring habitat formers. These studies have documented long habitat cascades from seagrass-bivalve-seaweed (Thomsen et al. 2013), bivalve-seaweed-snails-seaweed (Thomsen et al. 2016a), and bivalve-barnacle-tunicates (Yakovis and Artemieva 2017) interaction chains. Although these studies have documented that long habitat cascades do exist, they were carried out on small spatio-temporal scales (Thomsen et al. 2016a, Thomsen et al. 2013) or only reported impacts on a few targeted inhabitant species (Thomsen et al. 2016a, Yakovis and Artemieva 2017). It remains unknown whether long habitat cascades are unique or general processes that affect only a few species or entire communities of inhabitants.

Here, my aim is describing a new long bivalve-seaweed-seaweed habitat cascade and testing if (i) the third order habitat former modifies entire communities (instead of only affecting a few target species), (ii) the third order habitat former increases biodiversity, and (iii) these processes operate across a range of environmental conditions (here, biomass levels of the secondary habitat formers, seasons, elevation levels, sites and estuaries). These research

questions were addressed in estuaries on the South Island of New Zealand, where I had observed that the bivalve *Austrovenus stutchburyi* can provide attachment substrate for the coarsely branched seaweed *Gracilaria chilensis*. The seaweed, in turn, can provide substrate for the sheet-forming seaweed *Ulva* sp., that potentially further modify communities of small mobile invertebrates (Hawes and Smith 1995, Thomsen et al. 2016a).

3.3 MATERIALS AND METHODS

3.3.1 Observational study

An observational study was carried out to test if the abovementioned bivalve-seaweed-seaweed habitat cascade affect invertebrate communities across seasons and study sites and with different biomass levels of the secondary habitat former *Gracilaria chilensis* (hereafter *Gracilaria*). Samples were collected at two sites (Site 1, 43°33'17.5"S 172°43'16.3"E, 3.2 km from estuary mouth; Site 2, 43°33'16.1"S 172°43'03.2"E, 3.8 km from estuary mouth) in winter (2015) and summer (2016) in the Avon-Heathcote Estuary in the South Island of New Zealand. At each sampling event, *Austrovenus stutchburyi* (hereafter *Austrovenus*) was collected with small (< 6 cm frond length; 0.15 ± 0.02 gDW) and large (> 10 cm frond length; 0.55 ± 0.07 gDW) attached *Gracilaria*, with and without attached *Ulva* sp. (hereafter *Ulva*). I also collected 'control' *Austrovenus* without any attached seaweed. *Austrovenus* were collected during low tide with a swift movement (Alkarkhi et al. 2008, Baudrimont et al. 2003) from the mid intertidal zone (n = 6 per test factor combination, *Austrovenus* is easy to collect because its shell apex protrudes a few mm out from the sediment surface). *Austrovenus*¸ with or without attached seaweed, were immediately added to a plastic bags and transported to the lab for processing.

3.3.2 Manipulative experiment

In a manipulative experiment, I tested if the physical structure of co-occurring biogenic habitat formers facilitates invertebrates and if results are consistent between sites and elevation levels. This experiment was done using abiotic mimics of all three habitat-forming species (Fig. 3.1C-F). A 3D model of a representative live *Austrovenus* (35 mm length) was created from 78 photos covering different angles of the shell, in Autodesk Memento. Three different sizes (30, 32, 35 mm length) were printed with a Da Vinci 1.0A 3D printer to mimic typical cockle sizes at the study site. These mimics are morphologically very similar to live *Austrovenus* and dead shells, but made of plastic instead of calcium carbonate. *Gracilaria* mimics (20 cm = 1.13

gDW, Fig. 3.1C-E) were made from red/white plastic twine, cut, twisted and wrapped to provide a shape that mimicking the coarsely branched red alga. Mimics were then tied to a u-bent 20 cm metal peg pushed into the sediment. Finally, *Ulva* mimics were made of green plastic flagging tape (5 cm = 0.15 gDW, Fig. 3.1D-F) and four mimics were attached to a *Gracilaria* mimic that again were tied onto an *Austrovenus* mimic. A plastic twine was also attached to the *Gracilaria* mimics and a u-bent 20 cm metal peg inserted into the mud to prevent the loss of the samples from tidal currents and waves. *Austrovenus* mimics with and without attached *Gracilaria* or *Gracilaria-Ulva* mimics were inserted into the sediment (partially covered to simulate the natural position of live cockles) at two sites (see observational study) in both the shallow subtidal and mid intertidal zone (n = 3). Mimics were out-transplanted on late April and collected two months later as described for the observational study.

3.3.3 Natural experiment

Finally, I tested, in a natural experiment, if long habitat cascades can be found in different estuaries in the South Island of New Zealand. In pilot experiments, I had observed that *Ulva* often attached to my *Gracilaria* mimics, highlighting that the mimics simulated the physical structure of *Gracilaria*. I therefore out-transplanted 6 mimics to both intertidal mudflats and intertidal seagrass beds in the Nelson Haven estuary (41°13’56.81S, 173°18’38.23E), Delaware Bay (41°9’59.78S, 173°26’33.56E) and Avon-Heathcote Estuary (43°33'17.5"S 172°43'16.3"E) between October and November 2016, hoping that some (but not all) would be inhabited by *Ulva*. Ca 8-10 weeks later, a core was collected (0.0064 m^2, 10 cm into the sediment) around each peg and mimic, washed in the field in 1-mm mesh bags to retain mimics, seaweeds and macrofauna, before being transported to the lab. For my analysis, samples were grouped into mimics with no (or very little) vs high biomass of epiphytic *Ulva*. *Ulva* abundance was not manipulated or controlled, so these data represent a ‘natural experiment’ (Gerber and Green 2008).

3.3.4 Laboratory analysis

Samples from the observational study and the manipulative experiment were rinsed into a 250 μm sieve (i.e., the shell collections), whereas samples from the natural experiment were rinsed in a 1000 μm sieve (i.e., the sediment cores) to retain invertebrates associated with the different habitat-forming species. Seaweeds were detached from their hosts and weighed after drying at 55°C for 48 h or until no further weight loss could be detected. Retained invertebrates were

counted and large organisms were identified to species whereas small inconspicuous species were identified to Order or Family under a dissecting microscope at 40× magnification, and preserved in 70% ethanol.

3.3.5 Statistical analysis

I tested for treatment effects on (i) total abundances, (ii) taxonomic richness, and (iii) multivariate community structure. Multivariate community data were square-root transformed to reduce the importance of a few highly dominant taxa. The three responses were analyzed with permutational-based factorial analysis of variance (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. All factors were treated as fixed. Note that 'Site' was evaluated as a fixed factor because S1 (nearer to the ocean) and S2 (nearer to the river mouth) were positioned along a typical estuarine gradient with predictable differences in salinity, turbidity, nutrients and sediment characteristics (Skilton 2013). Similarly, I interpreted the three sampled estuaries to represent a gradient in anthropogenic disturbances, where the Avon-Heathcote Estuary is surrounded by Christchurch (population size of ~400,000), Nelson Haven is situated close to Nelson (~50,000) and Delaware Bay is in a rural area (with a few scattered houses). Finally, effects of *Ulva* attached to *Gracilaria* (GU) were compared to effects of *Gracilaria* alone (G) across the three data sets in a single quantitative analysis. Hedges *g* was calculated, as a standardized effect size, for each matching pair of 'G vs GU' treatments (cf. the matching grey and black bars in Fig. 3.2, 3.4 and 3.6) as $[(GU - G) / S] \times J$, where S is the pooled standard deviation and J is a factor that corrects for bias associated with small sample sizes (see Borenstein et al. 2009). A standard meta-analysis was carried out on abundance and richness data separately, using weighted random effect models, assuming that summary statistics have both sampling error and a true random component of variation in effect sizes between studies (Borenstein et al. 2009).

3.4 RESULTS

The observational study showed, as hypothesized, more invertebrates in the presence of epiphytic *Ulva* (4.52 ± 3.77 ind. per cockle) than without (3.00 ± 2.33) ($F_{1,85} = 3.65$, $p = 0.05$, Table 3.1) and at high (5.22 ± 3.93) compared to low (3.98 ± 0.92) *Gracilaria* biomasses ($F_{1,85} = 43.67$, $p = 0.001$), irrespective of site conditions or season (i.e., all other test conditions were

non-significant) (Fig. 3.2A, Appendix 3-3.1, 3-3.2, 3-3.3 for corresponding PERMANOVA tables). However, for richness, I only found more taxa with (4.52 ± 0.20 taxa per cockle) than without (3.00 ± 0.38) epiphytic *Ulva* at site 2, but not site 1 (*Ulva* × Site; $F_{1,85} = 4.35$, $p = 0.043$, Fig. 3.2B). In addition to these positive effects of *Ulva*, I also found significantly more taxa in summer ($F_{1,85} = 7.82$, $p = 0.007$), at high *Gracilaria* biomasses ($F_{1,85} = 10.41$, $p = 0.005$) and at site 2 ($F_{1,85} = 4.73$, $p = 0.025$) (Fig. 3.2B). *Ulva* had strong community-wide effects ($F_{1,85} = 5.61$, $p = 0.001$) although they, like for taxonomic richness, varied across sites (*Ulva* × Site; $F_{1,85} = 3.45$, $p = 0.001$). Communities also varied significantly, like richness, between seasons ($F_{1,85} = 3.06$, $p = 0.012$), *Gracilaria* biomasses ($F_{1,85} = 8.71$, $p = 0.001$) and site conditions ($F_{1,85} = 4.20$, $p = 0.001$) (Fig. 3.3).

In contrast to the observational study, where I found positive effects of live *Ulva*, I found such no effect on invertebrate abundances when artificial *Ulva* mimics were added to *Gracilaria* mimics (all effects were non-significant, Fig. 3.4A-B). However, there were significant *Ulva* × Elevation × Site interactions for both richness ($F_{1,85} = 5.50$, $p = 0.027$, Table 3.1) and community structures ($F_{1,85} = 3.43$, $p = 0.026$), suggesting complex effects on entire invertebrate communities from the *Ulva* mimics (Fig. 3.5, no other interactions, except Elevation × Site, were significant).

In the natural experiment, I found again, as hypothesized and documented in the observational study, more invertebrates in the presence of epiphytic live *Ulva* (5.33 ± 1.94 ind. $core^{-1}$) than without (4.25 ± 1.21) ($F_{1,64} = 6.06$, $p = 0.015$, Table 3.1). In addition, I also found a significant effect of Estuary on abundances ($F_{1,64} = 6.54$, $p = 0.006$, Fig. 3.6A) and a complex 3-factorial *Ulva* × Habitat × Estuary effect on richness ($F_{1,64} = 4.44$, $p = 0.023$), where the latter result suggests that *Ulva* does affect richness, but that these effects vary between seagrass beds, mudflats and estuaries. *Ulva* also significantly affected the community structures ($F_{1,64} = 2.67$, $p = 0.01$), as did Habitat ($F_{1,64} = 2.20$, $p = 0.028$) and Estuaries ($F_{1,64} = 7.95$, $p = 0.001$) whereas all interactions were non-significant ($p > 0.05$).

Finally, the analyses carried out across all data sets confirmed that *Gracilaria* with *Ulva* attached had significantly higher invertebrate abundances compared to *Gracilaria* without *Ulva* (Hedges' $g = 0.411$, 95% CI = 0.094-0.729, $p = 0.011$, Qm = 12.87). However, although the overall net effect on richness was also positive, this effect size was not significantly different from zero (Hedges' $g = 0.137$, 95% CI = -0.305-0.579, $p = 0.544$, Qm = 32.57).

3.5 DISCUSSION

In this study I documented a new example of a 'long' habitat cascade and I compared it with the similar lower-level habitat cascade, demonstrating that a tertiary habitat former increases invertebrate abundance and modifies community structure. These findings support a few previous published examples of increased facilitation arising from long habitat cascades (Thomsen et al. 2016a, Thomsen et al. 2013, Yakovis and Artemieva 2017).

Most studies on facilitation and habitat cascades have tested if the addition of a secondary habitat former increases biodiversity compared to when a primary habitat former exists on its own (Altieri et al. 2007, Altieri et al. 2010, Angelini and Silliman 2014, Bishop et al. 2012, Bishop et al. 2013, Bishop et al. 2009, Thomsen et al. 2010, Watson 2002). These studies have typically found higher abundances and more taxa of inhabitants when habitat-forming species co-exist although exceptions to this rule exist (Adams et al. 2004, Holmquist 1997). Here, I found strong support for a typical second-order habitat cascade because both richness and abundances generally were much higher when *Austrovenus* was inhabited by *Gracilaria* compared to when *Austrovenus* was collected alone (Fig. 3.2, 3.4). This strong cascade is thereby very similar to cascades involving other *Gracilaria* species attached to the snail *Batillaria australis* (Thyrring et al. 2015, Thyrring et al. 2013), the tubes of the polychaete *Diopatra cuprea* (Thomsen 2010), or the byssal threads of the mussel *Mytilus edulis* (Thomsen et al. 2013), and confirms the importance of seaweeds as important habitat formers in estuarine sedimentary systems (Bates 2009, Bishop et al. 2012, Bishop et al. 2013, Cordero et al. 2012, Johnston and Lipcius 2012, Koivisto and Westerbom 2010, Langtry and Jacoby 1996, Norkko 1997, Norkko and Bonsdorff 1996b, c, Raffaelli et al. 1998a, Thomsen et al. 2010). Compared to *Gracilaria*, *Austrovenus* and many other bivalves are mostly covered by mud, thereby limiting attachment for many sessile species (Gribben et al. 2009, Yakovis and Artemieva 2017, Yakovis et al. 2005) and making it an adverse habitat for mobile epifauna like many amphipods and snails. The small substrate area exposed above the sediment surface explains why I only found (beside *Gracilaria*) a few attached limpets and barnacles on *Austrovenus*. By comparison, *Gracilaria* offers a number of additional ecological niches and functions (Cordero et al. 2012, Johnston and Lipcius 2012, Thomas et al. 1998). For example, *Gracilaria* has a complex morphology with a large surface and interstitial spaces that facilitates invertebrates of various species and sizes (Buschmann et al. 1997, Nyberg et al. 2009, Thomsen 2010). Furthermore, *Gracilaria* may also provide a direct food sources for herbivores (Anderson et al. 1998, Anderson et al. 1993, Mancinelli and Rossi 2001) or an indirect food resource because

Gracilaria can provide habitat for readily digestible diatom communities (Fletcher 1995, Wang et al. 2017). Finally, the many interstitial spaces may also provide protection against predation for species such as juvenile crabs and spider crabs (this study), as shown for other juvenile crabs inhabiting the invasive seaweed *G. vermiculophylla* (Johnston and Lipcius 2012, Wright et al. 2014).

It is well documented that *Gracilaria* increase small scale levels of biodiversity in sedimentary systems because it increases habitat space and habitat complexity (see above references). However, expectations about how epiphytic *Ulva* (on *Gracilaria*) affects biodiversity in these systems is more complicated. For example, the sheet-forming *Ulva* is morphologically simpler than *Gracilaria* and probably provides less hiding places (Munari et al. 2015). This was supported by my results because net community effects were highly variable across different environmental conditions and only came across as clearly facilitative when I analysed effects across the entire data set (and only for abundances). Yet, although not observed in this study, *Ulva*'s 'flat habitat' may provide a new habitat for invertebrate species that are poorly adapted to the tubular and branching pattern of *Gracilaria* (branched vs sheet-forming; Beck 1998, Beck 2000, Chemello and Milazzo 2002, Colman 1940, Kostylev et al. 1997, Seed and O'Connor 1981, Taylor and Cole 1994). More importantly, *Ulva* typically has higher nitrogen content, less secondary metabolites and less rigid cell wall components and it is therefore more palatable compared to *Gracilaria* (Cruz-Rivera and Hay 2001, D'Antonio 1985, Grahame 1973, Hagerman 1966, Kamermans et al. 2002, McBane and Croker 1983, Pederson and Capuzzo 1984, Poore 1994, Watson and Norton 1987). These differences may explain why I found more invertebrates in the presence of epiphytic *Ulva,* in particular of the herbivorous snail *Micrelenchus* and herbivorous amphipods. Indeed, when I eliminated trophic subsidies by using *Ulva* mimics, I found, as expected, that herbivorous invertebrates were no longer facilitated (Bologna and Heck 1999, Boström and Mattila 1999, Gartner et al. 2013, Viejo 1999). Nevertheless, even though this tertiary habitat former modified community structures and facilitated herbivorous invertebrates, effects were less dramatic than the facilitation effect derived from the secondary habitat former (*Gracilaria*). Although few studies have documented similar long habitat cascades (Thomsen et al. 2013, Yakovis and Artemieva 2017), it is likely, given the high prevalence of facultative epibionts for marine sessile species (Wahl and Mark 1999), that many more undocumented examples exists, particularly in benthic rocky systems where available hard substrates and number of epibiontic species are much higher than in estuarine systems.

It has previously been discussed whether long habitat cascades increases stability of invertebrate communities (Yakovis and Artemieva 2017). However, I observed here that *Ulva* could change biomass rapidly, partly due to new colonization and fast growth and partly because its thallus often breaks off. Furthermore, during growth, *Ulva* drag increases, increasing the risk of dislodgment of (or from) *Gracilaria* or entrainment of the entire cockles-seaweed association (that then drifts around with the tidal currents) (Hawes and Smith 1995, Lutaenko and Levenets 2015). I suggest that, although relatively common in estuaries in New Zealand, this particular long habitat cascade may be less stable than other long habitat cascades (Thomsen et al. 2016a, Yakovis and Artemieva 2017). Indeed, given that hydrodynamic drag increases disproportionally with increasing seaweed biomass (Hawes and Smith 1995), *Gracilaria* will eventually dislodge over time. I finally suggest that hydrodynamic forces and biomechanical size-drag-constraints ultimately will limit the stability of many other long habitat cascades (Gaylord et al. 1994, Hawes and Smith 1995, Thomsen 2004).

I conclude that a tertiary habitat-forming epiphytic seaweed, in a long habitat cascade, altered communities and increased abundances of invertebrates. In addition, I found this long habitat cascade under a wide range of environmental conditions, although with highly varying effects ranging from strong facilitation to inhibition of invertebrates. Based on these results and a growing number of observations from systems where epibiosis is common, I suggest that many other 'long' habitat cascades are likely to exist, and I encourage more research into these processes to better understand how co-existing habitat-forming species affect invertebrate communities.

Tables

Table 3.1 Overview of PERMANOVA reporting the results of the factorial analysis. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Values represent the contribution of each test factor to the total variability of the PERMANOVA models ($\eta^2 = SS_{Explained}/SS_{Total}$). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. See Appendix 3-3.1, 3-3.2, and 3-3.3 for complete PERMANOVA tables. Significant values are in bold (*: p = 0.05-0.01, **: p = 0.01-0.001, ***: p < 0.001).

Factors	Abundance	Richness	Community structure
Observational study			
Ulva (Ulv)	**2.81%***	0.07%	**5.35%*****
Gracilaria biomass (Bio)	**33.62%*****	**9.48%****	**8.30%*****
Site (Si)	0.10%	**4.31%***	**4.01%*****
Season (Sea)	1.07%	**7.13%****	**2.92%***
Ulv × Bio	0.33%	1.66%	1.23%
Ulv × Si	2.02%	**3.96%***	**3.29%*****
Ulv × Sea	0.93%	0.06%	1.52%
Bio × Si	0.03%	1.91%	1.09%
Bio × Sea	0.98%	1.84%	0.74%
Si × Sea	1.27%	0.09%	0.43%
Ulv × Bio × Si	0.36%	1.93%	1.14%
Ulv × Bio × Sea	0.83%	2.61%	1.39%
Ulv × Si × Sea	0.28%	0.64%	0.67%
Bio × Si × Sea	1.42%	0.45%	0.66%
Ulv × Bio × Si × Sea	0.06%	0.08%	0.52%
Manipulative experiment			
Ulva (Ulv)	0.63%	5.33%	5.17%
Elevation (Ele)	0.70%	2.35%	4.01%
Site (Si)	4.89%	15.35%	1.84%
Ulv × Ele	1.39%	0.68%	5.81%
Ulv × Si	10.23%	0.19%	7.30%
Ele × Si	0.39%	5.94%	**13.84%****
Ulv × Ele × Si	10.51%	**17.94%***	**10.94%***
Natural experiment			
Ulva (Ulv)	**7.65%***	1.88%	**3.29%****
Habitat (Hab)	1.01%	**6.59%***	**2.71%***
Estuary (Est)	**16.49%****	**27.23%*****	**19.57%*****
Ulv × Hab	2.80%	0.46%	1.06%
Ulv × Est	2.74%	2.24%	2.62%
Hab × Est	1.88%	1.00%	2.35%
Ulv × Hab × Est	0.58%	**8.69%***	3.17%

Figures

Figure 3.1 The cockle *Austrovenus stutchburyi* provides substratum for the red seaweed *Gracilaria chilensis* that again provides substrate for the green seaweed *Ulva* sp., as seen on mudflat (A) and a close-up in the laboratory (B). Experimental transplant for short (C-E) and long (D-F) habitat cascades for the manipulative experiment with mimics of *Austrovenus*, *Gracilaria* and *Ulva*, in laboratory (C-D) and field (E-F) settings. Experimental transplant of *Gracilaria* mimics with low and high biomass (G) that facilitated natural colonization of *Ulva* (H).

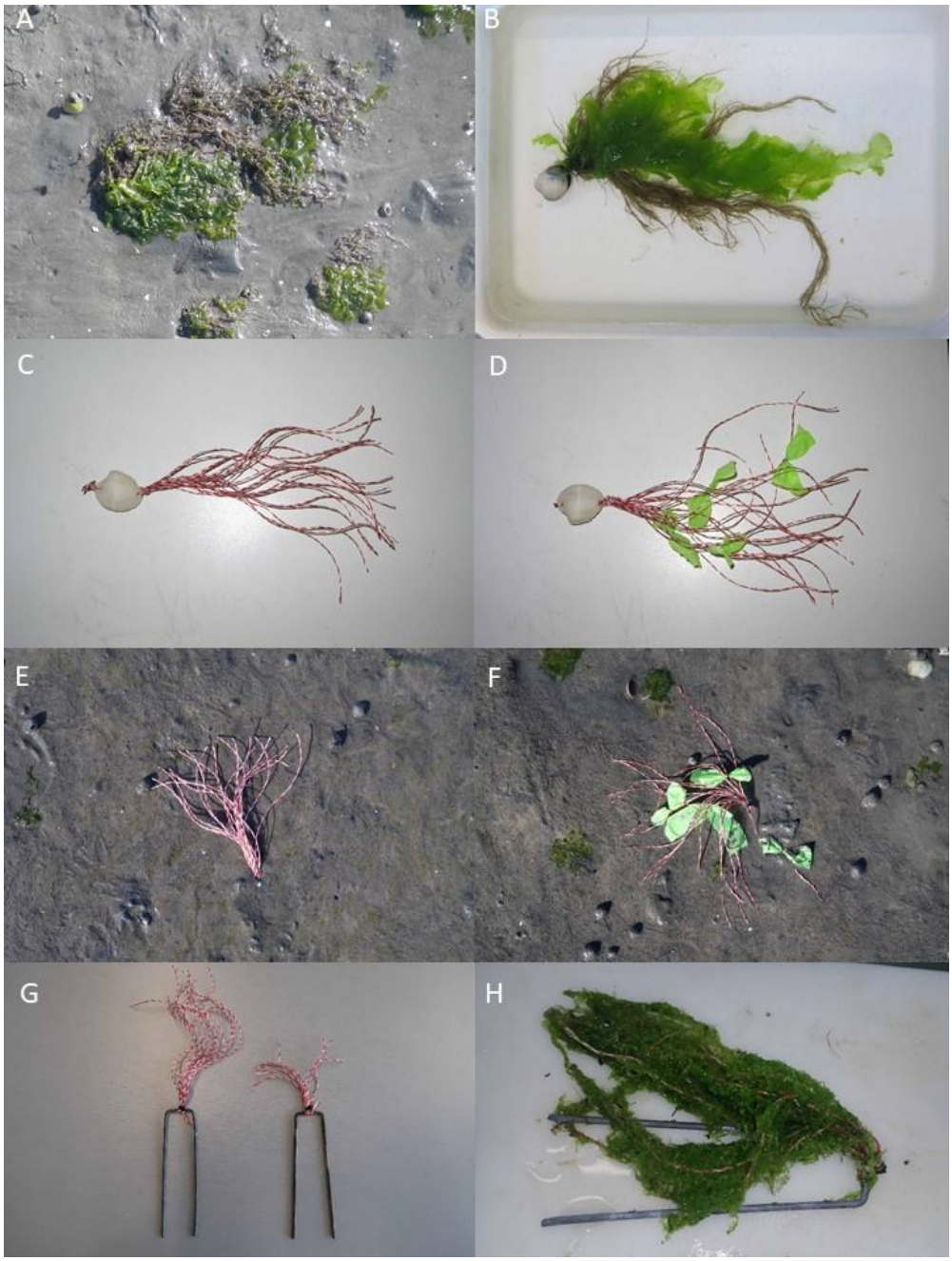


Figure 3.2 Observational study, testing for effects of *Ulva* sp. (U) attached to *Gracilaria chilensis* (G) in low (L) and high (H) biomasses, attached to *Austrovenus stutchburyi* (A) on abundance (Fig. A) and richness (Fig. C) of invertebrates in summer and winter at two sites. Error bars = 1 SE, n = 6.

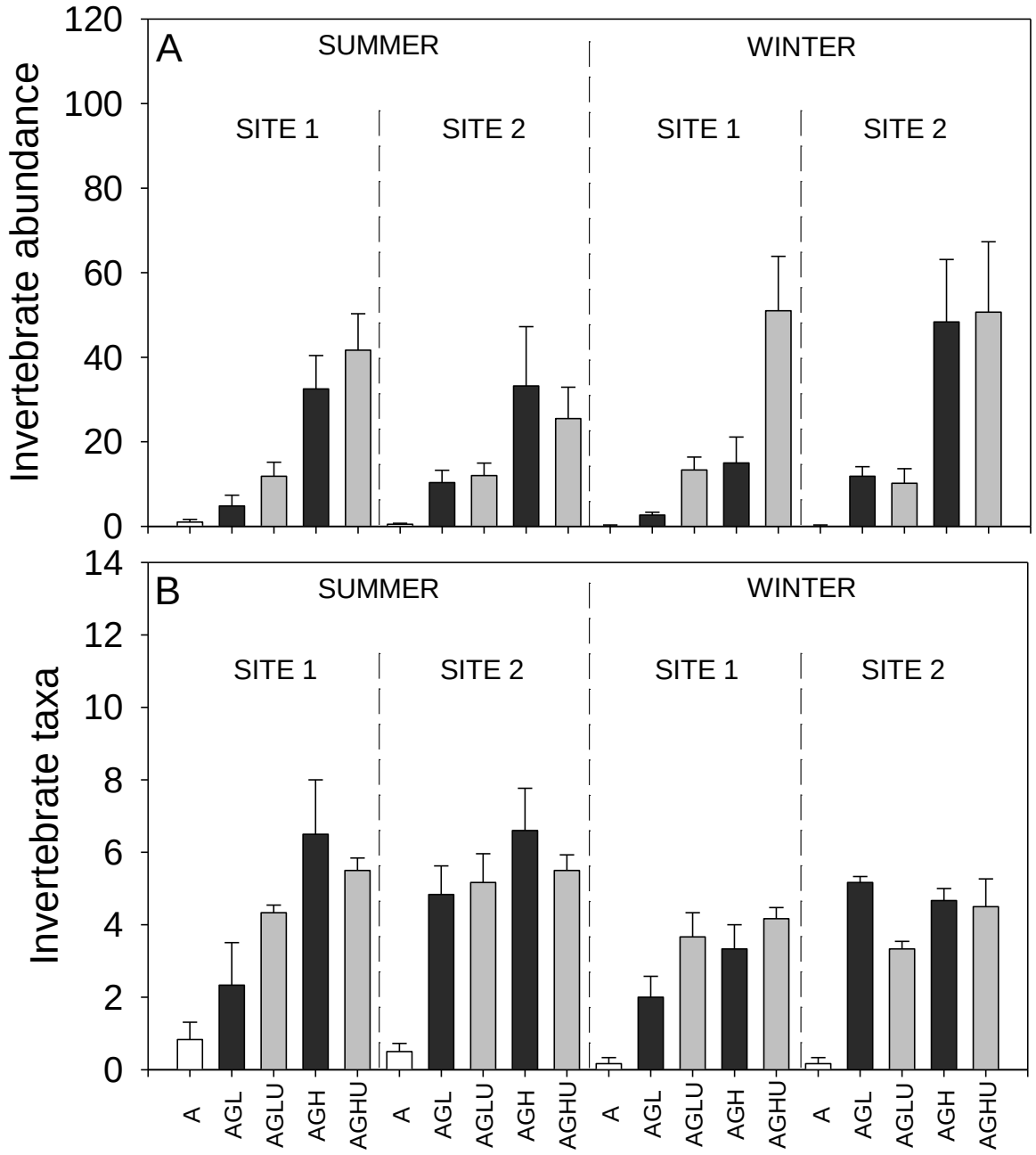


Figure 3.3 Observational study, testing for effects of *Ulva* sp. (U) attached to *Gracilaria chilensis* (G) in low (L) and high (H) biomasses attached to *Austrovenus stutchburyi* (A) on multivariate invertebrate community structures in summer (A) and winter (B). The test factor 'Site' was pooled. For simplicity, data were split into summer and winter but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). MDS plots were based on square root transformed data and the Bray-Curtis similarity coefficient. A SIMPER analysis was used to determine which species contributed up to 75% of the data variability (1: amphipods spp., 2: *Halicarcinus whitei*, 3: *Micrelenchus tenebrosus*, 4: *Diloma subrostrata*, 5: juvenile crabs). Stress: 0.16. Of the 24 collected *Austrovenus* shells without attached seaweed, 8 were inhabited by at least 1 invertebrate (points shown on plots) but 16 were not (16 points in coordinate -1.4, 0.1).

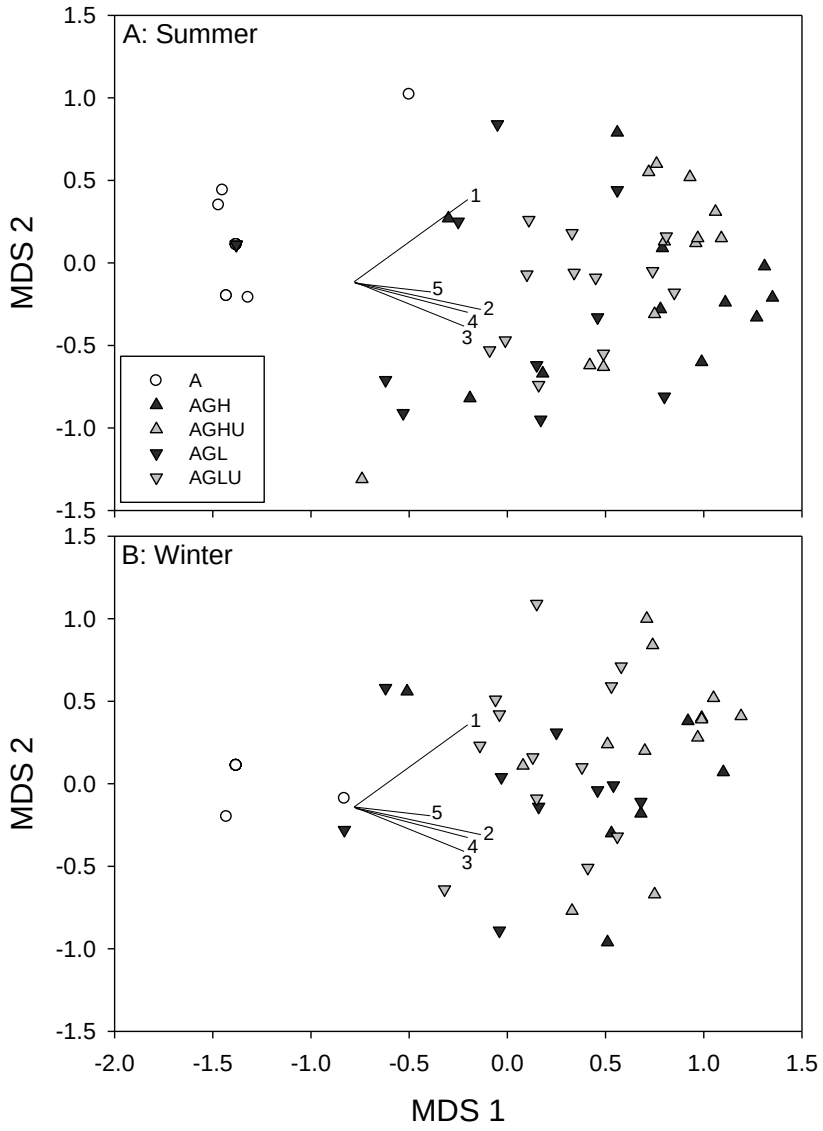


Figure 3.4 Manipulative field experiment, testing for effect of *Ulva* sp. (U) attached to *Gracilaria chilensis* (G) attached to *Austrovenus stutchburyi* (A) on abundance (Fig. A, B) and richness (Fig. C, D) of invertebrates at two sites and two elevation levels. Error bars = 1 SE, n = 3. ND = no data as these cockles were lost in a storm. In this experiment, *Austrovenus*, *Gracilaria* and *Ulva* were all non-living mimics.

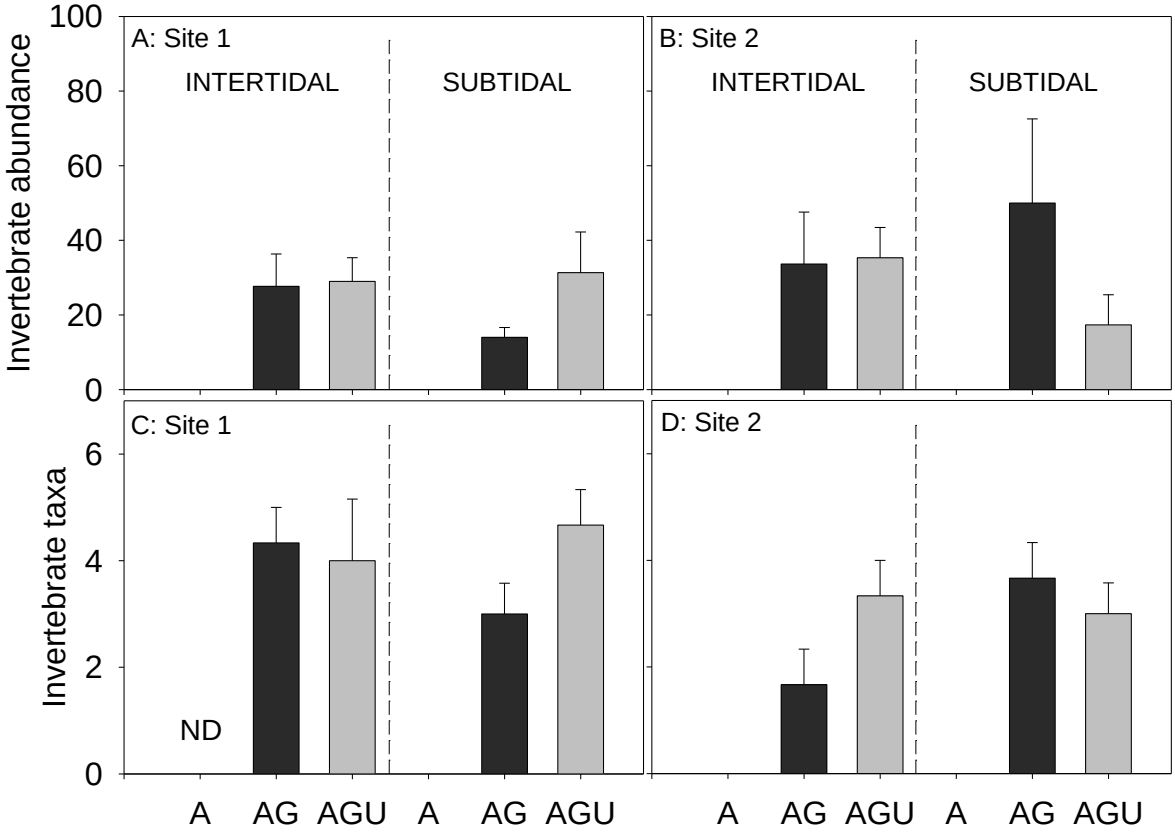


Figure 3.5 Manipulative field experiment, testing for effects of *Ulva* p. (U) attached to *Gracilaria chilensis* (G) attached to *Austrovenus stutchburyi* (A) on multivariate invertebrate community structures at two elevation levels and two sites. MDS plots were based on square root transformed data and Bray-Curtis similarity coefficient. A SIMPER analysis was used to determine which species contributed up to 75% of the data variability (1: *Micrelenchus tenebrosus*, 2: amphipods spp., 3: *Halicarcinus whitei*, 4: *Diloma subrostrata*). Stress: 0.14. None of the 12 collected *Austrovenus* were inhabited by invertebrates.

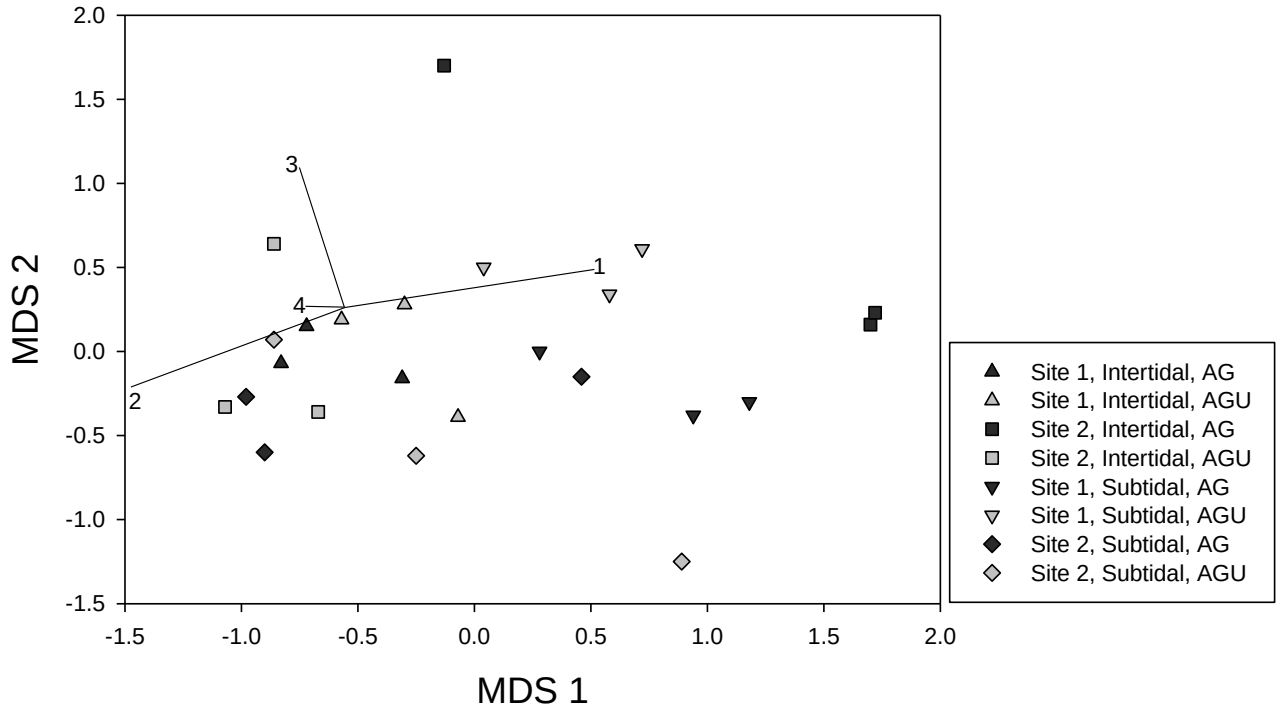


Figure 3.6 Natural experiment, testing for effects of *Ulva* (U) attached to *Gracilaria* mimics (G) on the abundance (A) and richness (B) of invertebrates in two habitats (Mudflat vs *Zostera* bed) and three estuaries (Avon-Heathcote, Delaware Bay, Nelson Haven). Error bars = 1 SE, n = 6.

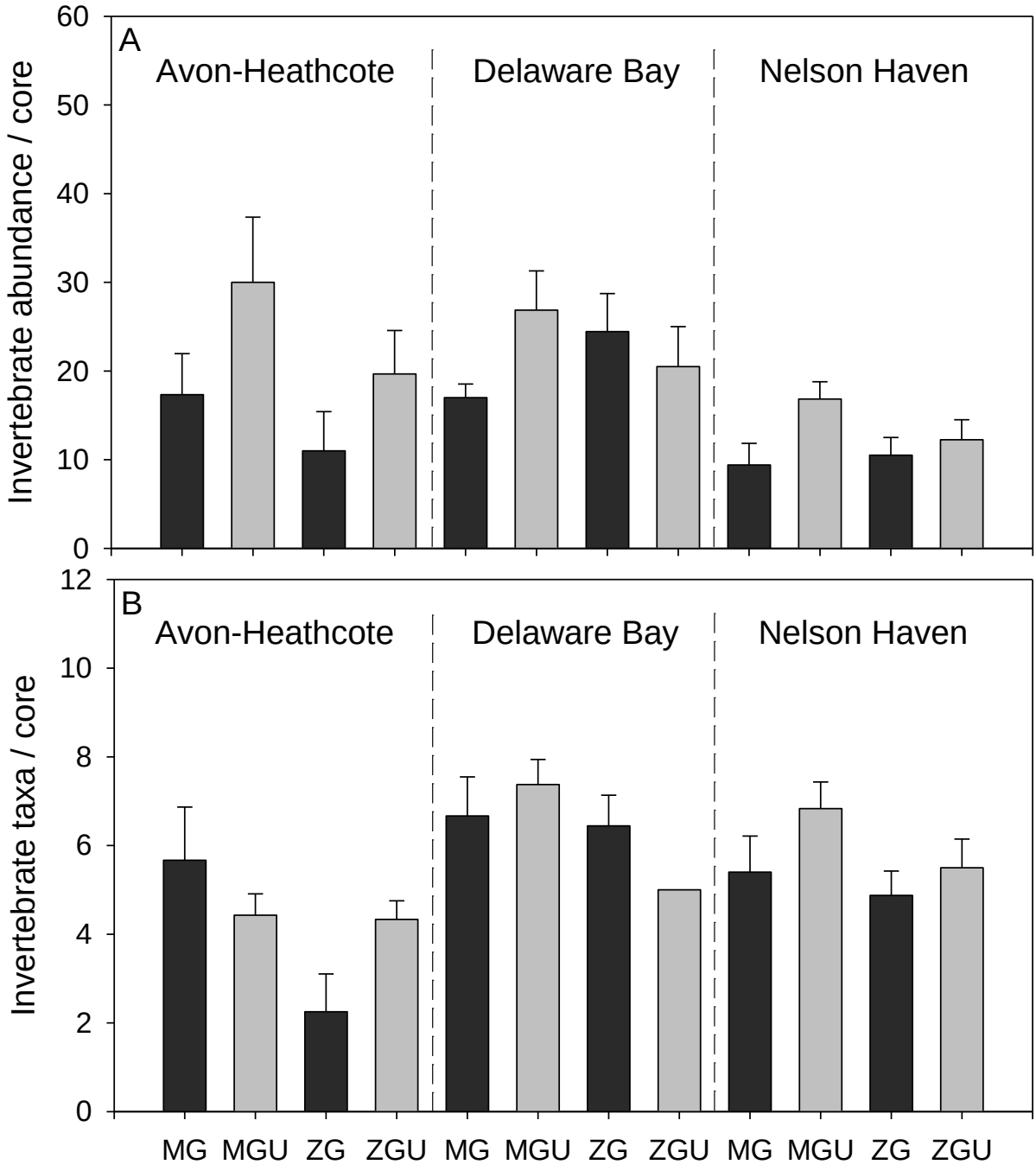
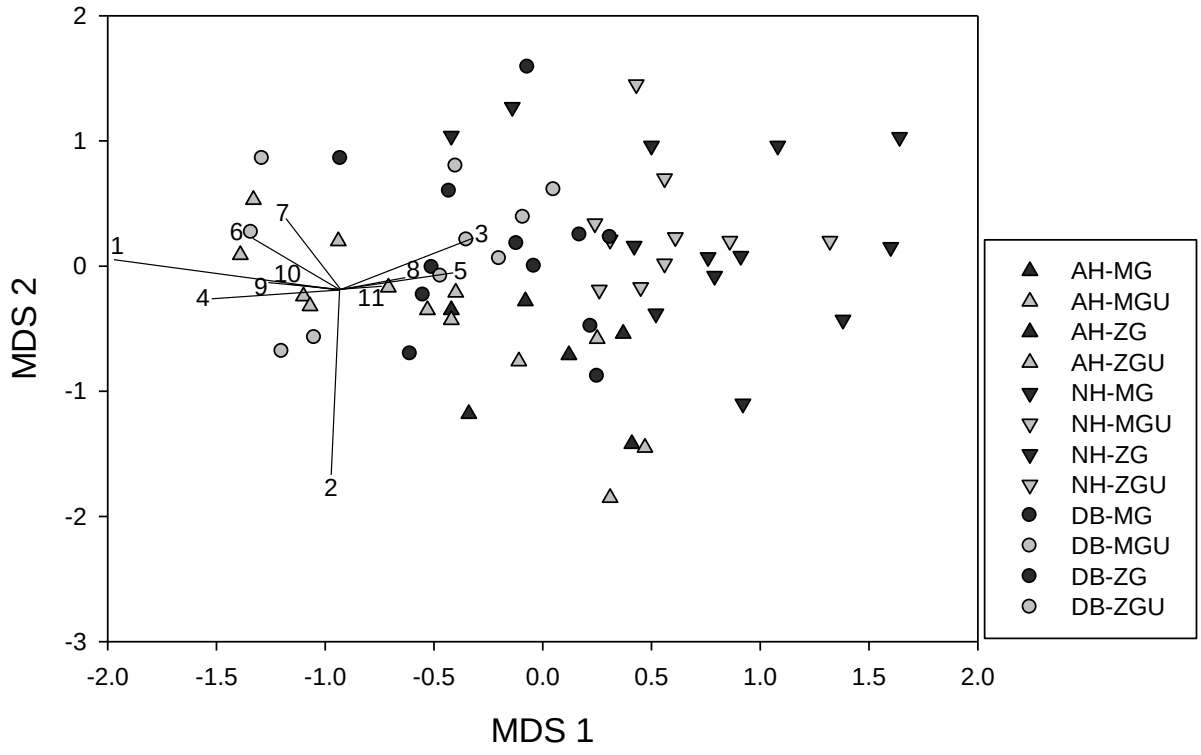


Figure 3.7 Natural experiment, testing for effects of *Ulva* sp. (U) attached to *Gracilaria chilensis* mimics (G) on multivariate invertebrate community structure in two habitats (Mudflat vs *Zostera* bed) and three estuaries (Avon-Heathcote, Delaware Bay, Nelson Haven). MDS plots were based on square root transformed data and the Bray-Curtis similarity coefficient. A SIMPER analysis was used to determine which species contributed up to 75% of the data variability (1: *Micrelenchus tenebrosus*, 2: errantia polychaetes, 3: *Spisula aequilatera*, 4: *Hemigrapsus crenulatus*, 5: sedentaria polychaetes, 6: *Notoacmea helmsi*, 7: *Halicarcinus whitei*, 8: *Macomona liliana*, 9: *Anthopleura aureoradiata*, 10: *Diloma subrostrata*, 11: *Austrovenus stutchburyi*). Stress: 0.25. One outlier sample was removed from the plot (AH-ZT with coordinates 8.0, 0.0).



CHAPTER 4: The role of drifting seaweeds in habitat cascades in seagrass beds

4.1 ABSTRACT

Seagrasses are marine plants that take up nutrients, stabilize sediments, increase habitat complexity and thereby increase the biodiversity of sedimentary coastal ecosystems. Seagrasses can also facilitate the local abundance of drifting seaweeds that become entangled around their leaves and stems. Little is known about how co-occurring seagrasses and seaweeds affect seagrass-associated fauna, but it is possible that the addition of seaweeds increases biodiversity by providing additional or novel habitat in a process known as a 'habitat cascade'. I tested the hypotheses that (i) the presence of seaweeds entangled in estuarine seagrass beds modifies biodiversity via cascading habitat formation, (ii) similar processes occur across a wide range of spatial and temporal conditions, and (iii) the biomass and the structural attributes of seaweeds (comparing living vs artificial mimics of seaweeds) modify the strength of habitat cascades. Cores collected in seagrass beds with and without entangled seaweeds from a latitudinal gradient and a seasonal survey confirmed the first two hypotheses; entangled seaweeds consistently increased the abundance and taxonomic richness of invertebrates in seagrass beds. The third hypothesis was tested in a field experiment that demonstrated stronger facilitation of invertebrates in high than low seaweed biomass and by live than mimic seaweeds. Furthermore, a final large-scale field experiment using different seaweed mimics showed consistent facilitation of invertebrates with increasing mimic biomass between estuaries and across latitudes, thereby supporting my hypotheses from a single experimental setting. In concert, these results show that entangled seaweeds, by adding biomass and different physical structures, can support strong habitat cascades in soft-bottom estuarine seagrass beds.

4.2 INTRODUCTION

Seagrasses are ecologically important foundation species that provide complex habitat compared to adjacent unvegetated sediments in estuarine and shallow coastal ecosystems around the world (Boström and Bonsdorff 1997, Connolly 1997, Currás et al. 1994, Edgar 1990a, Ferrell and Bell 1991, Orth 1973, Peterson 1982, Stoner 1980b). Indeed, seagrasses provide a wide range of ecosystem services, including modifying local hydrodynamics (Hemminga and Duarte 2000, Orth et al. 2006), buffering waves and currents (Heiss et al. 2000), taking up and storing carbon (Fourqurean et al. 2012), filtering nutrients (Short 1987),

and providing food and shelter to seagrass-associated flora and fauna (Abele 1974, Boström and Bonsdorff 1997, Hall and Bell 1988, Heck Jr and Orth 1980, Heck et al. 1995, Kohn 1967, Stoner and Lewis 1985). The abundance and diversity of macrofauna are usually positively correlated with the biomass of seagrass (Brook 1978, Heck Jr and Orth 1980, Lewis III and Stoner 1983, Stoner 1980b) and respond to variation in vegetation cover (Lewis III 1984, Virnstein and Howard 1987) as a result of different microhabitat structures within seagrass beds (Lewis III 1984, Stoner 1980a).

However, seagrass are not the only macrophytes in sedimentary estuaries, as seaweeds can be abundant and contribute significantly to primary production. Indeed, seaweeds may have many similarities to seagrass as they also affect ecosystem functions such as environmental buffering, filtering of nutrients and providing habitat to invertebrates. However, estuarine seaweeds differ from seagrass in that they require a hard substrate for initial attachment of early life stages, and by having a morphological holdfast structure that provides support to withstand currents and waves (Biber 2007). Nevertheless, for many estuarine seaweeds, these holdfast attachment structures and/or seaweed stipes and fronds are biomechanically weak compared to hydrodynamic peak tides and storm waves (Thomsen 2004), often resulting in dislodgement or pruning of seaweed fronds (Vahteri et al. 2000). For example, green opportunistic and fast growing sheet-forming *Ulva* species and slower growing coarsely branched *Gracilaria* species are common in estuaries throughout the world, often found attached to small rocks or shells (Fletcher 1996, Round 1981, Thomsen 2004). These seaweeds often break off from their substrate (Hawes and Smith 1995, Thomsen 2004) and thereby become 'drifting' seaweeds. Drifting seaweeds are subsequently transported with tidal currents and can be deposited high on the beach as wrack, in deep channels (Norkko et al. 2000) or in seagrass beds (Cummins et al. 2004, Holmquist 1997, Huntington and Boyer 2008) because seagrass reduces tidal currents and stems and leaves provide physical structures for entrapment (Halling et al. 2013, Thomsen 2010).

Entrapped seaweeds can have drastic effects on seagrasses and seagrass-associated macrofauna by physically smothering them (Adams et al. 2004, Bell and Westoby 1987, Holmquist 1997), reducing light availability (Hauxwell et al. 2001), producing toxic substances through decomposition processes (Hauxwell et al. 2001, Krause-Jensen et al. 1996, McGlathery et al. 1997, Thybo-Christesen et al. 1993), and decreasing oxygen levels (Norkko and Bonsdorff 1996a, b, c). However, some studies have shown that a relatively low biomass of drifting seaweed entangled within seagrass beds can have positive effects on invertebrate communities (Cardoso et al. 2004, Holmquist 1997, Hull 1987, Raffaelli et al. 1998a, Stoner

and Lewis 1985, Thomsen 2010). For example, drifting seaweeds may provide more structure and habitat (Holmquist 1994, Kulczycki et al. 1981, Schneider and Mann 1991b), increase habitat complexity (Langtry and Jacoby 1996, Norkko 1997, Norkko and Bonsdorff 1996b, c, Raffaelli et al. 1998a, Vetter 1995), and increase colonization area for new settlement of juvenile invertebrates (Norkko et al. 2000). Furthermore, seaweeds in seagrass beds also provide trophic resources and refuges from predators (Heck Jr 1979, Heck and Thoman 1981, Holmquist 1994, Holmquist 1997, Norkko 1998, Vetter 1998, Virnstein and Carbonara 1985, Virnstein and Howard 1987, Wilson et al. 1990b) and facilitate invertebrate dispersal between seagrass patches as they are passively transported in tumbling drift weeds (Highsmith 1985, Holmquist 1994, Kingsford 1992).

More recently, cumulative effects on invertebrates from entangled seaweeds in seagrass beds have been reinterpreted in the context of cascading habitat formation, a type of facilitation cascade that emphasises habitat formation as a driving ecological force (Altieri et al. 2007, Angelini et al. 2011, Thomsen and Wernberg 2014, Thomsen et al. 2010). In cascading habitat formation co-existing primary and secondary habitat-forming species facilitate inhabitant species, compared to monocultures of the primary habitat-forming species. For example, Thomsen (2010) showed that the seagrass *Zostera marina* was a primary habitat formers, that promoted entanglement of the drifting seaweed *Gracilaria vermiculophylla* (secondary habitat former), and the two habitat-forming species in concert increased richness, diversity and density of local invertebrates. Similar examples have been described in the past for other seagrass species, including *Thalassia testudinum* (Adams et al. 2004, Bologna and Heck 1999, Leber 1985), *Amphibolis antarctica* and *Amphibolis griffithii* (Edgar and Robertson 1992), and *Zostera noltii* (Cardoso et al. 2004). However, these studies were generally not considered in the context of habitat cascades and typically were done only at a single location with a single type and biomass level of entangled seaweed. It therefore remains unknown how general these processes are over wider spatio-temporal scales and to what extent seaweed attributes (e.g., abundance or physical structure) modify the effect on seagrass-associated invertebrates. Additionally, as described in Chapter 2, few studies have compared habitat cascades with morphologically different secondary habitat formers from the same ecosystem (Bishop et al. 2009, Hughes et al. 2014) or have used mimics of habitat formers to test the effects of morphology on local invertebrates (but see Bologna and Heck 1999, Schneider and Mann 1991b).

Here, I address this research gap by testing whether the presence of entangled seaweeds modifies the abundance, richness and community structure of seaweed-associated macrofauna.

I also test if the abundance (i.e., biomass) and attributes (whether it is alive or an artificial mimic) of the entangled seaweeds affect the strength of habitat cascades, and if results are consistent across a wide range of environmental conditions (here latitudes, elevation levels and seasons).

In this study, the primary habitat former is *Zostera muelleri* (hereafter *Zostera*) the only seagrass species in New Zealand (Short et al. 2007). *Zostera* is common in estuaries, intertidal sand-flats (Den Hartog 1970) and sheltered rocky shores in the intertidal and shallow subtidal zones (Inglis 2003). The secondary habitat former is predominately the drifting seaweed *Ulva* sp. (hereafter *Ulva*). *Ulva* is a sheet-forming opportunistic fast-growing green algae (Littler and Littler 1980) that can form large and dense drifting mats (Fletcher 1996, Jones et al. 2005). Note, however, that *Ulva* can also exist alone without seagrass on estuarine mudflats either being attached to bivalve shells or drifting around on the shallow mudflats (Fletcher 1996, Jones et al. 2005, Thomsen 2004). When found outside the seagrass habitats, *Ulva* can therefore also be considered a primary habitat-forming species. Many other species can have similar 'dual roles' as both a primary or secondary habitat former, depending on the habitat the species occupies. For examples, many seaweed species are primary habitat formers on rocks or sediments but can also function as secondary habitat formers when they are (i) entangled around seagrass (Adams et al. 2004, this study, Holmquist 1997, Thomsen et al. 2012a, Thomsen et al. 2013) (ii) attached to seagrass (Edgar and Robertson 1992) or (iii) entangled or attached to saltmarshes (Thomsen et al. 2009), mangroves (Bishop et al. 2012, Bishop et al. 2013) and other seaweed species (Armitage and Sjøtun 2016, Thomsen et al. 2016b, Viejo and Åberg 2003). Other organisms such as mussels and oysters, can also be sampled both as primary habitat formers on rocks or sediments and as secondary habitat formers when they are embedded within seagrass (Valentine and Heck Jr 1993), saltmarshes (Altieri et al. 2007, Altieri et al. 2010, Angelini et al. 2015) or attached to mangrove prop-roots (Hughes et al. 2014, McAfee et al. 2016). Typically, factorial experiments are applied to disentangle the relative importance of a habitat-forming species' dual ecological functions, by crossing at least two levels (presence-absence) of both the primary and the secondary habitat formers (and typically analysed with factorial ANOVA) (Adams et al. 2004, Altieri et al. 2007, Altieri et al. 2010, Bishop et al. 2012, Bishop et al. 2013, Thomsen et al. 2013). For simplicity, in this study I generally refer to *Zostera* as the primary habitat former and to the drift seaweeds (in most cases *Ulva*) as the secondary habitat former, but acknowledge that seaweeds, sampled alone, could also be considered primary habitat formers. Collecting co-occurring primary and secondary habitat formers is critical in order to estimate the ecological effect of the seaweed

over the seagrass bed (such as moisture retention) which otherwise would be strongly underestimated.In this chapter, I tested seven hypotheses: (i) the presence of primary habitat-forming species (*Ulva* or *Zostera*) increases biodiversity compared to unvegetated mudflats (Allen 1992, Connolly 1997, Hosack et al. 2006, Mattila et al. 1999); (ii) the presence of a secondary habitat former (here, *Ulva*) in seagrass beds further increases biodiversity at the plot scale (Schneider and Mann 1991a, Thomsen et al. 2012a, Thomsen et al. 2013); (iii) these seagrass-seaweed habitat cascades occur over a wide range of spatio-temporal conditions, including across latitudes, elevation levels and seasons (Thomsen et al. 2010); (iv) habitat cascades are strong where desiccation stress is high (i.e., at northern warm latitudes, in warm summer months and at higher intertidal elevation levels) assuming that facilitation is strong under high stress as predicted by the Stress Gradient Hypothesis (SGH; Bertness and Callaway 1994, McAfee et al. 2016); (v) habitat cascades are strong when seaweeds are abundant and alive, thereby providing more shelter and more trophic resources (Bishop et al. 2012, Thomsen et al. 2010); (vi) habitat cascades are stronger when non-living seaweed mimics are morphologically 'complex' (branched) compared to morphologically 'simple' (flat) (Schneider and Mann 1991b); (vii) gastropods use secondary habitat-forming seaweeds, within seagrass beds, as a refuge from predators (Bourdeau and O'Connor 2003, Kohn and Leviten 1976, Wilson et al. 1990b). The first four hypotheses were addressed with a seasonal and a spatial survey where sediment cores were collected from mudflats and seagrass beds from the Avon-Heathcote Estuary, in Christchurch, New Zealand (seasonal survey) and 15 estuaries around the South Island of New Zealand (latitudinal survey). The fifth and sixth hypotheses were investigated with a manipulative experiment in the Avon-Heathcote Estuary and a large scale experiment at 6 estuaries along the east coast of the South Island, where abundance and structure of the artificial mimics of the secondary habitat formers were manipulated. The last hypothesis was tested with a field predation experiment.

4.3 MATERIALS AND METHODS

4.3.1 Study region

A large scale spatial survey was carried out in 16 estuaries along a latitudinal gradient, spanning 6 degrees (divided into estuaries sampled at 40-41°S, 43°S, and 45-46°S, hereafter North, Central and South), of the South Island of New Zealand (Appendix 3-4.1 for a list of estuaries, geo-coordinates, sample dates, and number of sampled replicates for different treatments). This survey was supplemented by a two-year seasonal survey in the Avon-Heathcote Estuary around

Christchurch, and three manipulative experiments (two conducted in the Avon-Heathcote Estuary and one in 6 estuaries representing the latitudinal gradient). The seagrass *Zostera* (primary habitat former) is common in most of the 16 sampled estuaries (but less common in Children's Bay, New River, and Catlins River). Seaweeds (secondary habitat formers), in particular *Ulva* sp. and *Gracilaria chilensis* (hereafter *Ulva* and *Gracilaria*, respectively), were also relatively common in most estuaries (Appendix 3-4.1). I also occasionally collected other seaweed species (e.g., *Lophothamnion* sp., and *Polysiphonia* sp.) in association with *Zostera*.

4.3.2 Spatial survey: effects of secondary habitat former across latitudes

A survey was done in 16 estuaries between February and October 2016 to test for interactive effects of primary and secondary habitat-forming species on biodiversity across tidal height and latitudes. The survey design included 2 levels of seagrass (± 1st HF, *Zostera*) × 2 levels of seaweed (± 2nd HF, *Ulva*) × 2 elevation levels (intertidal vs shallow subtidal) × 3 latitudes (North, Central and South) × 4-6 estuaries per latitude × 3 replicated cores. The collected seaweed was usually *Ulva*, but occasionally other seaweeds that are common secondary habitat formers were sampled if *Ulva* was absent (e.g., *Gracilaria*, *Lophothamnion* sp., *Polysiphonia* sp.; Appendix 3-4.1). Samples were collected randomly using a circular 9 cm inner diameter core (0.0064 m^2) pushed 10 cm down into the sediment. The core material was washed in the field in 1-mm mesh bags and then transported to the laboratory for processing. In this sampling scheme, *Ulva* can be considered both as a primary and secondary habitat former, depending on whether it was collected from the mudflat or from the seagrass bed, respectively.

4.3.3 Seasonal survey: effects of secondary habitat former across seasons

Seasonal variations in the effects of primary and secondary seaweeds on diversity were assessed in a 2-year survey from December 2014 to August 2016. Cores with and without *Ulva* were collected from seagrass beds at two sites on the eastern side of the Avon-Heathcote Estuary (close to Tern St. and Plover St., ca 500 m apart). The Tern St. site is closer to the estuary mouth and therefore typically has stronger currents, coarser sediments and experiences more marine conditions. The survey design was: 2 levels of seagrass (± 1st HF, *Zostera*) × 2 levels of seaweed (± 2nd HF, *Ulva*) × 2 elevations (intertidal vs shallow subtidal) × 2 sites Plover and Tern, ca 1.7 and 1.3 km from the Avon-Heathcote river mouth) × 2 seasons (summer vs winter) × 2 years × 4 replicated cores. Cores were collected as described for the spatial survey.

4.3.4 Experiment 1: effects of secondary habitat former type and biomass

This experiment tested if the biomass and biological attributes of entangled seaweeds affect the diversity of seagrass-associated invertebrates. More specifically, living seaweeds and artificial mimics were added to seagrass beds in low and high abundances. To test whether results were consistent in space and time, the experiment was repeated at two sites and two seasons. The experimental design was therefore: 2 'types' of seaweed (2^{nd} HF, *Ulva* or Mimic) × 2 'levels' of seaweed (2^{nd} HF biomass, low vs high) × 2 sites (Plover and Tern, ca 1.7 and 1.3 km from the Avon-Heathcote river mouth) × 2 seasons (summer vs winter) × 4 replicates. Additional control plots (without any *Ulva*) were established in the seagrass beds. Mimics were made from 2.5 cm wide green flagging tape, cut, twisted and wrapped to provide a shape that mimicked *Ulva* and tied to a u-bent 20 cm metal peg that was pushed flush into the sediment (Appendix 3-4.7). Pegs were also added to control plots as procedural controls. The added biomass of *Ulva* and mimics in the low and high treatments was 2.0 ± 0.1 and 5.6 ± 0.2 gWW for *Ulva* and 1.4 ± 0.0 and 5.2 ± 0.1 g for the mimic. The experiment was carried out ca 200 m out from Tern St. in the Avon-Heathcote Estuary, in July (winter) and November (late spring) 2016. The experiment ran for two weeks. At the end of the experiment a core was collected from each plot centre, as described for the surveys.

4.3.5 Experiment 2: effects of secondary habitat formers morphology across latitudes

The second experiment tested if non-living structures mimicking *Ulva* and *Gracilaria* morphologies increase diversity of seagrass-associated invertebrates. It was hypothesized that facilitation of invertebrates increases with the biomass of mimics and that facilitation occurs across latitudes and habitat types. This was tested with the following experimental design: 2 levels of seagrass (± 1^{st} HF, *Zostera*) × 2 types of seaweed mimics (flat Tape vs branched Twine) × 2 biomasses of seaweed (2^{nd} HF biomass, low vs high) × 2 elevations (intertidal vs shallow subtidal) × 3 replicates. Control plots without any mimics were established on the mudflat and adjacent seagrass bed. Mimics were made from red/white plastic twine (mimicking the branched *Gracilaria*) and green flagging tape (mimicking the flat *Ulva*, as described in the previous experiment), cut, twisted and wrapped to mimic the morphology of the seaweeds and tied to a u-bent 20 cm metal peg inserted flush with the sediment surface (Appendix 3-4.7). Again, pegs were also added to control plots to avoid confounding treatments. Seaweed mimics were added to plots as either 0.4 or 1.0 g of the branched mimic or 1.3 or 5.0 g of the flat mimic. The experiment was conducted in two estuaries in the central area of the South Island (Avon-Heathcote Estuary, in Christchurch, and Robinsons Bay, in Akaroa), two in the North (Nelson

Haven and Delaware Bay, close to Nelson) and two in the South (Portobello Bay and Papanui, close to Dunedin) (Appendix 3-4.1). The experiment was initialised between October and November 2016 and ran for 8-10 weeks (experimental run time varied slightly between the 6 estuaries). At the end of the experiment cores were collected as described for the surveys and experiment 1.

4.3.6 Experiment 3: effects of predators

Finally, I tested the hypothesis that seaweeds within seagrass reduce predation pressure on snails and, more specifically, that predation rates depend on the biomass and morphology of seagrass and seaweeds. To test this, 36 cages were added between a mudflat and a seagrass bed in the eastern part of the Avon-Heathcote Estuary (ca 300 m out from Tern/Plover St.). Cages were constructed from plastic containers (17×17×18 cm) from which the bottom was removed so that the cage could be pushed into the sediment (12 cm into the sediment, 5 cm protruding above the sediment surface). I drilled 36 1-mm holes in the side-walls of the containers so incoming and outgoing tides would fill and drain the cages following the natural tidal cycle (Appendix 3-4.8).

Each cage enclosed 13 *Micrelenchus tenebrosus* snails (potential crab prey) where the surface was covered with either mud, *Ulva* (in both low and biomass), *Zostera* or co-occurring *Zostera* and *Ulva* (the latter again in both low and biomass). The overall experimental design was: 2 predator levels (± 1 adult crab) × 6 habitats × 3 replicates. After adding 18 cages to a mudflat and 18 to an adjacent seagrass bed, 13 gastropods (8.3 ± 0.1 mm length) were added to each cage. *Ulva* biomass was added as 2.70 (low) or 3.70 (high) gWW biomass. Finally, 1 predatory crab (*Hemigrapsus crenulatus*, 25.9 ± 0.5 mm carapace width) was added to half of all the containers before they were covered with 1-mm mesh to contain the animals (Appendix 3-4.8). The experiment ran for 5 days in January 2017 and treatments were checked every 2 days to determine if crabs were present and alive. At the end of the experiment, crushed and living snails were counted, and the snail habitat occupancy was recorded as attached to either the cage side, mud, *Zostera* or *Ulva*.

4.3.7 Morphological traits of habitat formers

Morphological traits were quantified and compared between the different live species and mimics sampled in the surveys and experiments. Traits included surface area:dry weight ratios, fractal dimension, circularity (a measure of ‘roundness’, ranging from 0 for an infinitely elongated polygon, to 1 for a perfect circle; Sedgewick 2010) and lacunarity (Ferreira and

Rasband 2012, an index of ‘gappiness’ or ‘visual texture’, considered a measure of heterogeneity; Karperien 2007). Ten individuals of living *Zostera* and live and mimics of *Ulva* and *Gracilaria* were blotted three times with a paper towel and spread out on a white background to enhance the contrast for subsequent image analysis. A picture was taken of each sample with a Canon PowerShot G7X Mark II, using a ruler for scale. Each frond was then dried at 55°C for 48 h or until no further weight loss could be detected and its dry weight measured. Using Photoshop, each image was converted to grey scale and thresholded to binary images. Surface area:dry weight and circularity were calculated in ImageJ (Rasband 1997-2016), as was fractal dimensions and lacunarity, using the plugin FracLac (Karperien 1999-2013).

4.3.8 Laboratory analysis

In the laboratory, core samples were rinsed onto a 1-mm sieve to retain macroinvertebrates, seagrass and seaweeds. After pouring each sample into a plastic tray, seaweeds were identified and the seagrass was split into above (leaves) and below (rhizomes and roots) sediment tissue. All plant materials were weighed (gDW) after drying at 55°C for 48 h or until no further weight loss could be detected. All invertebrates were counted and identified to the lowest possible level (usually to species but sometimes to Order or Family) under a dissecting microscope at 40× magnification, and preserved in 70% ethanol. Invertebrates smaller than 1 mm (e.g., copepods and most amphipods) were therefore excluded from these analyses. Furthermore, repeated field and laboratory sieving was likely to have broken up fragile worm-like taxa that therefore may be under-represented in the analyses.

4.3.9 Statistical analysis

Treatment effects for the surveys and the first two experiments were analyzed for (i) total abundance, (ii) taxonomic richness, and (iii) multivariate community structure of invertebrates. Here data were square-root transformed to reduce the statistical importance of a few highly dominant species and to decrease variances for the most abundant taxa. Responses were analyzed with permutation-based factorial analysis of variance (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994) followed by post-hoc pair-wise t-tests (Anderson et al. 2008). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. Assumptions of normality and homogeneity of variances in the data sets were met. The control treatment (*Zostera* alone) was not included in the statistical analysis because the objective here

was testing for interaction effects between secondary habitat former type and biomass. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Results were considered significant if $p \leq 0.05$. Data from the field predation experiment (percentage of eaten gastropods and habitat preferences) were analyzed with a contingency table and chi-square tests. Morphological trait data were analyzed individually with Anova and combined with PERMANOVA, followed by post-hoc pair-wise t-tests, to test if traits differed between primary and secondary live and mimics of habitat-forming species.

4.4 RESULTS

4.4.1 Spatial survey: effects of secondary habitat formers across latitudes

Invertebrate abundance. A total of 6,827 invertebrates from 37 taxa were counted from 458 cores. The most abundant were the trochid *Micrelenchus tenebrosus* (1,497 individuals), the gastropod *Potamopyrgus estuarensis* (1,343) and the bivalve *Austrovenus stutchburyi* (1,253).

Seven interactions were statistically significant, suggesting many complex effects between spatial gradients and presence of habitat-forming species (Table 4.1). Most of the interactions, however, explained little of the data variability ($\eta^2 = SS_{Explained}/SS_{Total}$). The largest of the η^2 values was for the 2nd HF × Estuary interaction, which only accounted for < 5% of data variability. Presence of both primary (Z > M and ZS > S, Fig. 4.1A-C, except ZS = S in Fig. 4.1B) and secondary (S > M and ZS > S, Fig. 4.1A-C) habitat formers significantly increased the abundance of invertebrates ($p = 0.001$) although the strength of facilitation varied with latitude. More specifically, the significant three-factor interaction 2nd HF × 1st HF × Latitude ($p < 0.05$, but $\eta^2 = 0.5\%$) showed that cores with seaweeds contained more invertebrates in central latitudes (S and ZS, Central > North = South), mud cores contained more invertebrates in the north (M, North > Central = South) while invertebrates associated with *Zostera* alone did not change across latitudes (Fig. 4.1A-C). All the single test factors, except Elevation, were significant and Estuary alone (nested in Latitude) explained almost 50% of the data variability. This test factor is, however, ecologically less interesting because it simply reflects that abundances of invertebrates vary in space. Importantly, I found consistent evidence for habitat cascades with significant positive effect of seaweeds within seagrass beds across latitudes (ZS > S, Fig. 4.1A-C), and with slightly stronger effects in central regions where seaweeds doubled the amount of invertebrates.

Invertebrate richness. There were three significant interactions on richness but they accounted for little data variability (η^2 < 5%, Table 4.1). The most important 2-way interaction (1st HF × Estuary) accounted for 3.3% of variability ($p < 0.01$), reflecting that, although the presence of *Zostera* generally increased the number of taxa compared to mud cores (Fig. 4.1D-F), the magnitude of facilitation varied between estuaries. The Elevation × Estuary interaction explained less 3% of the data variability. Richness was significantly higher in the presence of seaweeds (ZS = S > Z > M, Fig. 4.1D-F) and at northern estuaries (North > Central > South, Fig. 4.1D-F). All the single test factors were significant and Estuary again explained most of the data variability (η^2 = 20%). As in the analyses of abundances, I found again evidence for habitat cascades across latitudes (ZS > S, Fig. 4.1D-F) with more taxa in cores with co-occurring seagrass and seaweeds compared to the seagrass alone.

Invertebrate community structure. A total of 11 interactions were significant (Table 4.1) where the interaction 1st HF × Estuary was the most important ($p = 0.001$, η^2 = 3.6%). Both the primary and secondary habitat formers interacted in a three-factor interaction with Estuary ($p = 0.001$, η^2 = 1.7%) and Latitude ($p < 0.01$, η^2 = 0.4%). The presence of both *Zostera* and seaweeds had strong effects on the community structure in most estuaries and across all latitudes. All the single test factors were highly significant ($p = 0.001$), where Estuary (nested in Latitude) again explained most of the data variability (η^2 = 35%), followed by Latitude itself (η^2 = 12%) (Fig. 4.2A-C, the remaining factors explained < 4%). An nMDS ordination plot indicated a separation of samples from northern, central and southern regions, showing more pronounced grouping of mud cores compared to cores with co-existing habitat formers (Fig. 4.2). Nine species accounted for 50% of the multivariate community variability. Both *Micrelenchus tenebrosus* and *Austrovenus stutchburyi* correlated positively with presence of co-existing habitat formers, whereas *Macomona liliana* and *Zeacumantus subcarinatus* correlated with monocultures of the habitat formers (Fig. 4.2).

4.4.2 Seasonal survey: effects of secondary habitat former across seasons

Invertebrate abundance. A total of 7,524 invertebrates from 23 taxa were counted from 254 samples. The most abundant invertebrates were *Micrelenchus tenebrosus* (5,339 individuals), *Austrovenus stutchburyi* (647) and errant polychaetes (401).

There were 9 significant interactions (Table 4.1), where 2nd HF × Season accounted for most of the data variability (η^2 = 4.6%). There was a significant 3-way interaction between

habitat formers and seasons (2^{nd} HF × 1^{st} HF × Season, $p < 0.01$, $\eta^2 = 1.0\%$), showing stronger invertebrate facilitation from both *Ulva* and *Zostera* in winter (Fig. 4.3B). All the single factors except Site were significant ($p = 0.001$), where the presence of the secondary habitat formers explained much of the variability ($\eta^2 = 30\%$). By contrast, presence of a primary habitat former only explained 12% of the data variability. Similar to the latitudinal survey, there was evidence of habitat cascades across seasons, as more invertebrates were in cores with co-occurring seagrass and seaweeds (ZU > Z), although *Ulva* had slightly stronger facilitation effects in winter (Fig. 4.3A-B).

Invertebrate richness. There were 6 significant interactions (Table 4.1), with Season × Year ($p = 0.001$) explaining 9.1% of the variability. Among the significant single factors, Year explained most of the data variability ($p = 0.001$, $\eta^2 = 8.9\%$), with more taxa being found in the first year of sampling (5.04 ± 0.18 taxa $core^{-1}$ vs 3.83 ± 0.14). The effects of the primary and secondary habitat formers were highly significant ($p = 0.001$), both factors explaining ca 12% of the data variability (the only interaction with a habitat former was 1^{st} HF × Year, $p = 0.001$, $\eta^2 = 2.8\%$). Richness was therefore positively affected by both *Zostera* (4.84 ± 0.15 vs 4.02 ± 0.18; Z = ZU > M = U; Fig. 4.3C-D) and *Ulva* (4.95 ± 0.17 vs 3.93 ± 0.16; U = ZU > M = Z, Fig. 4.3C-D). As for the abundance, there was evidence of habitat cascades in both seasons (ZU > Z, Fig. 4.3C-D), with more taxa found in presence of both habitat formers, but with stronger effects in summer than winter.

Invertebrate community structure. Of 13 significant interactions (Table 4.1), the most important (Season × Year, $p = 0.001$) only explained 2.1% of the total data variability. The 3-way interaction between the two co-occurring habitat formers and Season was again significant ($p < 0.01$, $\eta^2 = 0.9\%$), where pair-wise comparisons showed differences between all test factors combinations. All single factor tests were highly significant ($p < 0.001$), where the presence of the secondary habitat former explained most of the data variability ($\eta^2 = 11\%$), followed by presence of the primary habitat former ($\eta^2 = 6.8\%$) and Season ($\eta^2 = 5.6\%$). Seasonal effects could, in contrast to presence of primary and secondary habitat formers, not be visually distinguished on the nMDS ordination (Fig. 4.4). As in the spatial survey, *Micrelenchus tenebrosus* explained most of the community variability, correlating positively with presence of both *Ulva* and *Zostera* (Fig. 4.4).

4.4.3 Experiment 1: effects of secondary habitat former type and biomass

Invertebrate abundance. A total of 2,073 invertebrates from 18 taxa were counted from 80 samples. The most abundant were again *Micrelenchus tenebrosus* (1,186 individuals) and *Austrovenus stutchburyi* (607).

There were 5 significant interactions (Table 4.1), with most variability being explained by 2nd HF × Season ($p = 0.001$, $\eta^2 = 13.8\%$). There were significantly more invertebrates associated with living *Ulva* (53.38 ± 9.69 ind. core^{-1}) compared to *Ulva* mimics (22.88 ± 1.80), but this pattern was only observed in winter (UL = UH > ML = MH, Fig. 4.5B), and not in summer (ML = MH = UL = UH, Fig. 4.5A). Furthermore, the Type and Biomass of the secondary habitat former interacted significantly with Season in a three-factor interaction ($p < 0.05$, $\eta^2 = 2.6\%$). I found significantly more invertebrates on the living *Ulva* in high biomass compared to the mimics but, again, only in winter (UL-UH > ML-ML, Fig. 4.5B). Among the single test factors, Season explained most of the data variability ($\eta^2 = 30\%$), followed by Site ($p < 0.01$, $\eta^2 = 6.6\%$) and presence of secondary habitat former ($p = 0.001$, $\eta^2 = 5.9\%$). More specifically, there were more invertebrates in winter compared to summer (34.38 ± 4.62 vs 17.45 ± 1.22), more in cores from Plover than Tern sites, and in the presence of the secondary habitat former (the latter again demonstrating habitat cascades). However, habitat cascades were found only in winter and when seaweeds were alive compared to their mimics (Fig. 4.5B, UH > UL > MH = ML = O).

Invertebrate richness. The only factor significantly affecting invertebrate richness was the Site × Season interaction ($p < 0.05$, Table 4.1) as more taxa were found in cores from Plover than Tern sites, but only in summer.

Invertebrate community structure. Community structure was significantly affected by 5 interactions (Table 4.1), the most important of which was Site × Season ($\eta^2 = 6.5\%$). Among the single test factors, Season explained most of the data variability ($\eta^2 = 12.4\%$), followed by the secondary habitat former Type ($\eta^2 = 5.5\%$) and Site ($\eta^2 = 3.2\%$). The effects of Type was most visible in the nMDS plots in winter (Fig. 4.6B), showing a clear separation between samples with living and artificial secondary habitat formers. Half of the multivariate data variability was explained by 4 species with strong correlations between *Micrelenchus tenebrosus* and live secondary habitat formers and *Diloma subrostrata* and mimics (Fig. 4.6A-B).

4.4.4 Experiment 2: effects of secondary habitat former morphology across latitudes

Invertebrate abundance. In total, 3,963 invertebrates from 37 taxa were recorded from 313 samples. Samples were dominated by *Micrelenchus tenebrosus* (1,197 individuals) and *Austrovenus stutchburyi* (694).

I found 12 significant interactions (Table 4.1), where most data variability was explained by 2nd HF × Estuary (η^2 = 3.0%). There was also a significant 2nd HF × Latitude interaction ($p < 0.01$, η^2 = 2.1%), where post-hoc pair-wise comparisons showed that the *Ulva* mimic (tape) were inhabited by double the number of invertebrates compared to the *Gracilaria* mimic (twine) but only in the south (Fig. 4.7C). The 1st HF × Latitude interaction was also significant ($p < 0.05$, η^2 = 1.2%). Post-hoc comparisons revealed that more invertebrates were found in the mud samples compared to the *Zostera* samples from central and southern latitudes (Fig. 4.7B-C) and, for the *Zostera* treatments, more invertebrates in northern regions compared to central and southern regions (North > Central > South, Fig. 4.7A-C). Among the significant single factor tests, Latitude explained most of the data variability ($p = 0.001$, $\eta^2 > 27\%$) with more invertebrates in the northern regions (17.05 ± 0.94 ind. core^{-1}), compared to the central (13.11 ± 0.95) and the southern (6.32 ± 0.65) regions (Fig. 4.7A-C). In contrast to the surveys and experiment 1, there were significantly more invertebrates associated with the two types of mimics in the mud samples (13.80 ± 0.83) compared to *Zostera* samples (11.50 ± 0.76). The Biomass of the secondary habitat former also significantly affected invertebrate abundances ($p = 0.001$), highlighting that more invertebrates were associated with high than low seaweed biomass (16.05 ± 1.07 vs 11.71 ± 0.74). There was evidence for habitat cascades for both the *Ulva* and *Gracilaria* mimic types in the north, but only for *Gracilaria* mimics in the central region, and only for *Ulva* mimics in the southern regions (cf. the significant 2nd HF × Latitude interaction described before).

Invertebrate richness. I found 5 significant interactions (Table 4.1), explaining a total of ca 12% of the total data variability. The interaction between 1st HF × Elevation explained most of the data variability ($p < 0.01$, η^2 = 2.1%), demonstrating that more taxa were found in the subtidal zone in mud habitats but in the intertidal zone in *Zostera* habitats. The interaction between 2nd HF × Latitude was also significant ($p < 0.05$, η^2 = 2.0%), where more taxa were associated with *Ulva* mimics compared to *Gracilaria* mimics in central and southern regions (Ta > Tw, Fig. 4.7D-F, except Ta = Tw, Fig. 4.7D). For the single factor effects, most data variability was again explained by Latitude ($p = 0.001$, $\eta^2 > 30\%$), with more taxa in the

northern regions (6.09 ± 0.20 taxa core^{-1}), compared to the central (4.50 ± 0.18) and the southern (3.10 ± 0.20) regions (Fig. 4.7D-F). Furthermore, effects of the primary habitat former was highly significant ($p = 0.001$, $\eta^2 = 5.5\%$), again with more taxa associated with both type of mimics in mud compared to *Zostera* habitats (5.08 ± 0.19 vs 4.30 ± 0.17). There were also significantly more taxa in samples with tape compared to twine mimics (5.52 ± 0.20 vs 4.50 ± 0.20) and in samples with high compared to low biomass of the secondary habitat former (5.47 ± 0.21 vs 4.62 ± 0.19). Finally, I found evidence for habitat cascades for both types of mimics in the northern and central regions (Ta > Tw > M-Z, Fig. 4.7D-E), but only for *Ulva* mimics in the southern regions (Ta > M-Z, Fig. 4.7F).

Invertebrate community structure. Thirteen interactions were significant in the multivariate community analysis (Table 4.1), where Elevation × Estuary explained most of the data variability ($\eta^2 = 2.3\%$). Again, secondary habitat formers had a strong effect on the community structure, particular in central and southern latitudes (2nd HF × Latitude, $p < 0.01$, $\eta^2 = 1.1\%$). Among the single factor effects, 'Latitude' (again) explained most of the data variability ($\eta^2 = 25\%$), followed by Estuary ($\eta^2 > 10\%$), the primary and secondary habitat formers ($\eta^2 = 2.3\%$ and $\eta^2 = 1.5\%$, respectively), Elevation ($\eta^2 = 1.1\%$) and Biomass ($\eta^2 = 0.7\%$). The effect of latitude is evident from the nMDS ordination, with clear visual separation of samples collected from northern and southern regions. Half of the multivariate data variability was explained by 10 taxa, the most important of which were *Micrelenchus tenebrosus*, errant polychaetes, *Spisula aequilatera* and *Zeacumantus subcarinatus* (Fig. 4.8).

4.4.5 Experiment 3: effects of predators

Only 7 observed snails were crushed (i.e., 3.2% of all the snails that were exposed to predatory crabs). This result suggests that either *Hemigrapsus crenulatus* has low preference for small gastropods, that the crabs' chelae cannot peel or crush these shells, or that the gastropods can hide from predators within the aquatic plants. The chi-square test showed that gastropods were not associated with all habitats equally ($p < 0.001$, Appendix 3-4.6). In particular, in the *Ulva*-only addition treatments (where mud was also an abundant substrate), gastropods were found more on *Ulva* than on mud both in the presence (59.5%) and absence (73.6%) of crabs (Fig. 4.9). In the *Zostera*-only treatments (where mud again also was an abundant substrate) all gastropods were found attached to the seagrass leaves, both with and without crabs. Finally, in

the treatment that combined *Ulva* and *Zostera*, more snails were attached to *Ulva* in presence (60%) than absence (47.5%) of the crab.

4.4.6 Morphological traits of habitat formers

The PCO ordination showed a clear clustering of the different habitat formers, in particular separating living habitat formers from artificial mimics (Fig. 4.10, > 85% of the data variability was explained by the first two PCO axes) and all morphological traits were statistically significant ($p = 0.001$, Fig. 4.11). More specifically, the pair-wise comparison demonstrated significant differences between living *Ulva* and living *Gracilaria* for all morphological traits ($p = 0.001$), with *Ulva* having the highest fractal dimension while *Gracilaria* had the highest lacunarity (Fig. 4.11). I also found that the two seaweed mimics were significantly different from each other ($p = 0.001$), following a similar pattern as for living seaweeds (*Ulva* mimics had the highest fractal dimension while *Gracilaria* mimics the highest lacunarity). Additionally, comparing living seaweed with its own mimic showed that *Ulva* differed from its mimic only in circularity ($p = 0.004$) and surface area:dry weight ratio ($p = 0.002$), while *Gracilaria* differed from its mimic only for its surface area:dry weight ratios ($p = 0.007$). Finally, the seagrass was significantly different ($p = 0.001$) from the secondary habitat formers across all the tested morphological traits, where *Zostera* had lower lacunarity than *Gracilaria* and a lower fractal dimension than *Ulva* (Fig. 4.11)

4.4.7 Correlations

I found positive correlations between the abundance of invertebrates and the biomass of *Zostera* ($r_{Spearman} = 0.1$, $p = 0.003$, Fig. 4.12A) and *Ulva* ($r_{Spearman} = 0.18$, $p = 0.001$, Fig. 4.12B) as well as taxonomic richness and *Ulva* biomass ($r_{Spearman} = 0.27$, $p = 0.001$, Fig. 4.12D). However, there was no correlation between richness and *Zostera* biomass ($p > 0.05$, Fig. 4.12C).

4.5 DISCUSSION

This study documented that seaweeds entrained in seagrass beds facilitate invertebrates across latitudes, estuaries, sites, elevation levels, and seasons, thereby providing a strong case-study for the consistent occurrence of habitat cascades in seagrass beds.

4.5.1 Effects of habitat formers

My results demonstrated that single habitat formers support higher biodiversity than unvegetated sedimentary areas, that the seaweed *Ulva* provided a better habitat for invertebrates than the seagrass *Zostera* and that *Ulva* was ecologically important both as a primary and secondary habitat former. Firstly, both *Zostera* and *Ulva* consistently facilitated invertebrates compared to mudflat, thereby supporting past results from intertidal mudflats as demonstrated for seagrasses such as *Zostera muelleri* (Connolly 1997), *Z. marina* (Hosack et al. 2006, Mattila et al. 1999) and *Thalassia testudinum* (Arrivillaga and Baltz 1999, Uhrin and Holmquist 2003), and for seaweeds such as *Enteromorpha* spp. and *Gracilaria lemaneiformis* (Allen 1992), *Gracilaria vermiculophylla* (Ramus et al. 2017, Thomsen et al. 2013), and *Vaucheria subsimplex* (Bolam and Fernandes 2002). Many of these studies documented that facilitation arises by providing hard substratum and space for settlement, reducing desiccation stress and predation, and increasing food availability. Secondly, the stronger facilitation effect of *Ulva* compared to *Zostera* can be explained with their different morphological and anatomical traits. For example, *Ulva* could be a better habitat because of its higher fractal dimension and surface area:dry weight ratio compared to *Zostera* (this study) or because it is more palatable (Jorgensen et al. 2010, Marty-Rivera 2012). Similarly, the coarsely branched red seaweed *G. vermiculophylla* provided better predation refuge for juvenile crabs (*Callinectes sapidus*) and are inhabited by more invertebrates than *Z. marina*, probably because of a higher 3D-complexity (Johnston and Lipcius 2012, Thomsen et al. 2013). Finally, *Ulva* clearly also functioned as a secondary habitat former entrained in seagrass beds. Facilitation of invertebrates by *Ulva* within seagrass beds has, to my knowledge, only been shown once before (Thomsen et al. 2016a). This facilitation is probably a result of adding more biomass, complexity, food resources, predation shelter and by buffering abiotic stress, compared to *Zostera* without *Ulva*. These results support several other studies that have demonstrated invertebrate facilitation from different entrained seaweed species within seagrass beds such as *G. vermiculophylla*, *G. comosa* and *Laurencia* spp. (Gore et al. 1981, Holmquist 1997, Hooks et al. 1976, Pihl-Baden and Pihl 1984, Schneider and Mann 1991a, Thomsen et al. 2012a, Thomsen et al. 2013), even if these seaweeds often can have negative effects on the seagrass themselves (Holmquist 1997, Thomsen et al. 2013, Thomsen et al. 2012b).

4.5.2 Effects of latitude

A clear latitudinal gradient was found for invertebrate richness for both experimental and survey data, albeit with a less strong pattern for abundances, being highest in northern and

lowest in southern estuaries. Other studies have found correlations between latitude and invertebrate communities in seagrass beds (Heck and Wilson 1987, Nelson 1980, Virnstein et al. 1984). For example, Nelson (1980) found a negative correlation between amphipod density in *Z. marina* beds and latitude, potentially because lower latitudes can have higher predation pressure (Heck and Wilson 1987, Nelson 1980, Virnstein et al. 1984). However, in a review, Virnstein et al. (1984) argued that latitude is an inconsistent factor for predicting differences in the diversity of seagrass-associated invertebrates and that local controlling factors often have stronger effects.

4.5.3 Effect of season

I found interactions between season and presence of *Ulva* within seagrass beds in both the seasonal survey and the first experiment, but in contrast to my expectations, more invertebrates were found in winter than summer. Stressful winter conditions such as low temperatures and low food levels (like *Ulva*), could affect small scale spatial distribution of invertebrates, facilitating aggregation on and around high quality biogenic habitats like *Ulva*, compared to unvegetated mudflat (Allen 1992). However, other studies have found more invertebrates in summer in seagrass beds. For example, Duncan (2017) found more gastropods (including *Micrelenchus* spp. and *Diloma* spp.) in summer, supporting results from other seagrass species (Bloomfield and Gillanders 2005, Edgar 1990b, Nelson and Waaland 1997).

4.5.4 Structural and trophic effects of secondary habitat formers

This study highlighted that effects of non-living mimics were stronger on unvegetated mudflats than in seagrass beds, that live seaweeds can be better a habitat than mimics, that the morphology of mimics can affect invertebrate communities, and that effects of both live and mimic habitat-forming species are biomass-dependent. More invertebrates were found in cores were mimics where transplanted to mud than seagrass bed, probably because *Zostera* already provided basic ecological habitat-functions and thereby attenuated these types of effects (i.e., the mimics are, in part, functionally redundant). A similar result was found by Cardoso et al. (2004), comparing effects of *G. verrucosa* and *E. intestinalis* from a mudflat to a seagrass bed. Furthermore, invertebrate responses were structure-dependent as *Ulva* mimics were often inhabited by more invertebrates than the *Gracilaria* mimic. The seaweed mimics were reasonable morphological approximations of the living seaweeds as invertebrate abundances and richness were comparable with those found in the spatial survey for similar looking seaweeds. Still, I did find some differences in community structures between live and structural

mimics of *Ulva*, particularly in abundances of the herbivorous trochid snail *Micrelenchus tenebrosus*, one of the most abundant invertebrate species. *Micrelenchus* probably attaches preferentially to living *Ulva* to graze on it (Thomsen et al. 2016a). Other studies have found similar strong trophic subsidy effects (Bologna and Heck 1999, Boström and Mattila 1999, Gartner et al. 2013). For example, Hall and Bell (1988) found positive effects of both natural and artificial epiphytes on invertebrates inhabiting *T. testudinum*, Byers et al. (2012) found more epifauna on living fronds of *G. vermiculophylla* compared to plastic aquarium mimics on an intertidal mudflat, and Bologna and Heck (1999) documented more invertebrates on a seagrass mimic with natural epiphytes compared to mimics with artificial epiphytes. These studies all suggest that seaweeds can be an important food source for grazers inhabiting either mudflats or seagrass beds (Bologna and Heck 1999, Boström and Mattila 1999, Byers et al. 2012, Gartner et al. 2013, Hall and Bell 1988, Kitting et al. 1984, Orth and Van Montfrans 1984, van Montfrans et al. 1984). However, other species such as juvenile crabs, may be more likely to inhabit either live or mimic seaweeds to hide from predators or avoid physiological stress during low tide (Wilson et al. 1990a, b). Regardless of these results, however, colonization of artificial substrates by seagrass-associated invertebrates is clearly a common process (this study, Barber et al. 1979, Bell et al. 1985, Schneider and Mann 1991b, Virnstein and Curran 1986).

Finally, invertebrate responses correlated positively with the biomass of secondary habitat formers, as previously shown for *Ulva, Gracilaria* and other estuarine seaweeds (Byers et al. 2012, Drouin et al. 2011, Gore et al. 1981, Thomsen et al. 2016a, Thomsen et al. 2013). Similarly, the biomass of the seagrass also correlated positively with invertebrate abundances, supporting results from *Z. marina* seagrass beds (Attrill et al. 2000, Heck Jr and Wetstone 1977, Mattila et al. 1999), suggesting that facilitation associated with underpinning mechanisms such as habitat complexity, food provision and stress buffering, are density-dependent processes.

4.5.4 Effect of predation

It was here documented that an abundant estuarine crab (Jones et al. 2005) exerted very little predation pressure on trochid snails. The implication is that these snails are unlikely to inhabit *Zostera* or *Ulva* to avoid predation from local crabs. This result contrasts with other studies showing strong predatory impacts from congeneric *Hemigrapsus* species (Bourdeau and O'Connor 2003, Brousseau and Goldberg 2007, Keppel and Scrosati 2004). Still, it is possible that other invertebrates without hard shells such as amphipods, isopods, and juvenile crabs inhabit seaweeds and seagrass to avoid crab predation, as shown in many other studies

(Boström and Mattila 1999, Leber 1985, Wilson et al. 1990b), including *Z. marina*, *Ulva lactuca* (Wilson et al. 1990b) and other macroalgae in seagrass beds, both drifting (Adams et al. 2004, Leber 1985) and epiphytic (Williams et al. 2002). Furthermore, it is possible that larger organisms, like common wading birds and fish (Jones et al. 2005), are more important predators than crabs, and that *Ulva* and *Zostera* may still provide protection from these types of predators (Coen et al. 1981, Stoner 1979, Williams et al. 2002).

4.5.5 Conclusions

Although numerous studies have reported positive effects of seagrass, compared to unvegetated sediments, on invertebrate communities (see Boström et al. 2006 for a review), few studies have included specific tests of biomass effects (Attrill et al. 2000, Battley et al. 2011, Mattila et al. 1999, Thomsen et al. 2013). However, both Battley et al. (2011) and I found positive relationships between invertebrate abundances and *Z. muelleri* coverage in New Zealand and future studies should therefore include multiple densities of both the primary and secondary habitat formers. Furthermore, it is now well established that entrained seaweeds, even in relatively low biomass, can facilitate seagrass-associated invertebrate communities (Cardoso et al. 2004, Cowper 1978, Gore et al. 1981, Stoner and Lewis 1985, Thomsen 2010) but there is also evidence of deleterious effects on the seagrass itself if the seaweeds develop into extensive mats (Franz and Friedman 2002, Hauxwell et al. 2001, McGlathery 2001, Raffaelli et al. 1998a, Thomsen et al. 2012b). More studies should therefore aim to identify density-dependent thresholds (in both space and time) where effects of entrained seaweeds may shift from facilitation to inhibition of invertebrates.

This study documented that seaweeds entrained in seagrass beds, by adding biomass and different physical structures, create habitat cascades in soft-bottom estuaries across a wide range of environmental conditions.

Tables

Table 4.1 Overview of PERMANOVA reporting the results of the factorial analysis. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Values represent the contribution of each test factor to the total variability of the PERMANOVA models ($\eta^2 = SS_{Explained}/SS_{Total}$). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. See Appendix 3-4.2, 3-4.3, 3-4.4 and 3-4.5 for complete PERMANOVA tables. Significant values are in bold (*: p = 0.05-0.01, **: p = 0.01-0.001, ***: p < 0.001).

Factors	Abundance	Richness	Community structure
Spatial survey: effects of secondary habitat formers across latitudes			
2nd Habitat former (2HF)	**8.00%*** **	**7.33%*** **	**1.67%*** **
1st Habitat former (1HF)	**5.62%*** **	**4.36%*** **	**1.48%*** **
Elevation (Ele)	0.03%	**0.45%***	**0.51%*** **
Latitude (Lat)	**2.01%*** **	**15.52%*** **	**11.70%*** **
Estuary(Latitude) (Est(Lat))	**47.00%*** **	**19.77%*** **	**34.52%*** **
2HF × 1HF	**0.29%***	0.13%	**0.54%*** **
2HF × Ele	0.00%	0.03%	0.14%
2HF × Lat	**2.74%*** **	**0.73%***	**0.88%*** **
1HF × Ele	0.13%	0.03%	**0.21%***
1HF × Lat	**0.46%***	0.53%	**0.46%****
Ele × Lat	0.34%	0.21%	**0.93%*** **
2HF × Est(Lat)	**4.61%*** **	1.68%	**3.07%*** **
1HF × Est(Lat)	**1.96%****	**3.31%****	**3.58%*** **
Ele × Est(Lat)	**1.68%***	**3.00%***	**3.27%*** **
2HF × 1HF × Ele	0.02%	0.00%	0.01%
2HF × 1HF × Lat	**0.45%***	0.00%	**0.42%****
2HF × Ele × Lat	0.07%	0.44%	0.22%
1HF × Ele × Lat	0.00%	0.40%	0.29%
2HF × 1HF × Est(Lat)	0.58%	0.34%	**1.69%*** **
2HF × Ele × Est(Lat)	0.85%	0.88%	1.22%
1HF × Ele × Est(Lat)	0.71%	2.10%	**2.15%*** **
2HF × 1HF × Ele × Lat	0.28%	0.00%	0.25%
2HF × 1HF × Ele × Est(Lat)	0.19%	0.90%	0.76%
Seasonal survey: effects of secondary habitat former across seasons			
2nd Habitat former (2HF)	**31.27%*** **	**6.37%*** **	**10.54%*** **
1st Habitat former (1HF)	**11.53%*** **	**5.54%*** **	**6.78%*** **
Elevation (Ele)	**2.15%*** **	0.07%	**1.75%*** **
Site (Si)	0.01%	0.23%	**1.64%*** **
Season (Sea)	**6.31%*** **	0.62%	**5.64%*** **
Year (Yea)	**3.74%*** **	**8.88%*** **	**3.34%*** **
2HF × 1HF	0.50%	0.71%	**2.29%*** **
2HF × Ele	0.11%	0.00%	0.09%
2HF × Si	0.02%	0.25%	0.14%
2HF × Sea	**4.55%*** **	0.02%	**1.08%*** **

2HF × Yea	0.38%	0.25%	0.19%
1HF × Ele	0.09%	0.00%	**0.85%****
1HF × Si	0.37%	0.04%	0.43%
1HF × Sea	0.09%	0.62%	**0.56%***
1HF × Yea	0.08%	**2.78%*****	0.44%
Ele × Si	**2.20%*****	**2.68%****	**0.88%*****
Ele × Sea	0.00%	0.16%	0.10%
Ele × Yea	0.11%	**1.86%****	0.50%
Si × Sea	0.28%	0.01%	**1.10%*****
Si × Yea	0.04%	0.58%	**0.64%****
Sea × Yea	0.00%	**9.08%*****	**2.07%*****
2HF × 1HF × Ele	0.07%	0.01%	0.09%
2HF × 1HF × Si	0.19%	0.01%	0.30%
2HF × 1HF × Sea	**1.02%****	0.07%	**0.92%****
2HF × 1HF × Yea	0.40%	0.58%	0.31%
2HF × Ele × Si	**0.59%***	0.23%	0.19%
2HF × Ele × Sea	0.17%	0.01%	0.44%
2HF × Ele × Yea	0.00%	0.00%	0.37%
2HF × Si × Sea	0.28%	0.36%	0.18%
2HF × Si × Yea	0.17%	0.17%	0.20%
2HF × Sea × Yea	0.32%	0.01%	0.18%
1HF × Ele × Si	**0.73%***	0.55%	0.16%
1HF × Ele × Sea	0.03%	0.20%	0.20%
1HF × Ele × Yea	0.10%	0.16%	0.23%
1HF × Si × Sea	**0.60%***	0.02%	0.16%
1HF × Si × Yea	0.00%	0.03%	0.13%
1HF × Sea × Yea	**0.83%****	0.01%	0.47%
Ele × Si × Sea	0.19%	**1.31%***	**0.68%****
Ele × Si × Yea	**0.57%***	**1.51%***	0.48%
Ele × Sea × Yea	0.47%	0.05%	**0.90%****
Si × Sea × Yea	0.10%	0.47%	**0.76%****
2HF × 1HF × Ele × Si	0.35%	0.01%	0.08%
2HF × 1HF × Ele × Sea	0.06%	0.30%	0.28%
2HF × 1HF × Ele × Yea	0.04%	0.00%	0.38%
2HF × 1HF × Si × Sea	0.00%	0.84%	0.41%
2HF × 1HF × Si × Yea	0.04%	0.02%	0.18%
2HF × 1HF × Sea × Yea	**0.83%***	0.00%	0.50%
2HF × Ele × Si × Sea	0.32%	0.40%	**0.54%***
2HF × Ele × Si × Yea	0.27%	0.04%	0.12%
2HF × Ele × Sea × Yea	0.03%	0.06%	0.23%
2HF × Si × Sea × Yea	0.32%	0.06%	0.30%
1HF × Ele × Si × Sea	0.02%	0.05%	0.30%
1HF × Ele × Si × Yea	0.04%	0.21%	0.18%
1HF × Ele × Sea × Yea	0.00%	0.15%	0.46%
1HF × Si × Sea × Yea	0.02%	0.55%	0.23%
Ele × Si × Sea × Yea	0.00%	0.03%	0.15%
2HF × 1HF × Ele × Si × Sea	0.00%	0.02%	0.00%
2HF × 1HF × Ele × Si × Yea	0.13%	0.28%	0.32%
2HF × 1HF × Ele × Sea × Yea	0.07%	0.23%	0.22%
2HF × 1HF × Si × Sea × Yea	0.33%	0.02%	0.19%
2HF × Ele × Si × Sea × Yea	0.29%	0.04%	0.11%

1HF × Ele × Si × Sea × Yea	0.07%	0.14%	0.31%
2HF × 1HF × Ele × Si × Sea × Yea	0.00%	0.09%	0.30%
Experiment 1: effects of secondary habitat former type and biomass			
2nd Habitat former type (2HF)	**5.87%*** **	3.61%	**5.48%*** **
2nd Habitat former biomass (Bio)	0.86%	0.32%	0.44%
Site (Si)	**6.55%** **	1.27%	**3.22%***
Season (Sea)	**28.88%*** **	0.00%	**12.38%*** **
2HF × Bio	1.78%	2.53%	**2.69%***
2HF × Si	0.12%	3.26%	1.39%
2HF × Sea	**13.84%*** **	0.92%	**4.60%** **
Bio × Si	2.04%	0.05%	1.39%
Bio × Sea	**2.54%***	1.49%	1.29%
Si × Sea	1.21%	**6.55%***	**6.45%*** **
2HF × Bio × Si	**3.33%***	0.31%	**2.67%***
2HF × Bio × Sea	**2.59%***	1.87%	1.19%
2HF × Si × Sea	**3.07%***	6.02%	1.84%
Bio × Si × Sea	0.38%	0.00%	1.86%
2HF × Bio × Si × Sea	1.47%	0.21%	**2.51%***
Experiment 2: effects of secondary habitat former morphology across latitudes			
2nd Habitat former type (2HF)	0.21%	**5.28%*** **	**1.53%*** **
2nd Habitat former biomass (Bio)	**3.61%*** **	**3.61%*** **	**0.73%** **
1st Habitat former (1HF)	**4.05%*** **	**5.51%*** **	**2.25%*** **
Elevation (Ele)	0.11%	0.07%	**1.06%*** **
Latitude (Lat)	**27.19%*** **	**30.13%*** **	**25.49%*** **
Estuary(Latitude) (Est(Lat))	**8.32%*** **	**1.62%***	**10.74%*** **
2HF × Bio	0.12%	0.01%	**0.45%***
2HF × 1HF	0.08%	0.06%	0.36%
2HF × Ele	0.33%	0.05%	**0.53%***
2HF × Lat	**2.12%** **	**1.96%***	**1.06%*** **
Bio × 1HF	0.18%	0.02%	0.23%
Bio × Ele	0.00%	0.18%	0.15%
Bio × Lat	0.64%	0.20%	0.53%
1HF × Ele	**1.81%** **	**2.13%** **	**0.71%** **
1HF × Lat	**1.20%***	0.01%	**2.26%*** **
Ele × Lat	**1.49%***	0.63%	**0.95%** **
2HF × Est(Lat)	**3.03%** **	1.00%	**1.58%*** **
Bio × Est(Lat)	**1.55%***	0.67%	0.69%
1HF × Est(Lat)	0.17%	0.12%	**1.66%*** **
Ele × Est(Lat)	0.89%	**3.05%*** **	**2.33%*** **
2HF × Bio × 1HF	0.31%	0.40%	0.28%
2HF × Bio × Ele	0.12%	0.40%	0.32%
2HF × Bio × Lat	0.96%	0.84%	0.36%
2HF × 1HF × Ele	0.36%	0.01%	0.29%
2HF × 1HF × Lat	0.24%	0.16%	0.62%
2HF × Ele × Lat	0.84%	0.16%	0.53%
Bio × 1HF × Ele	0.06%	0.53%	0.31%
Bio × 1HF × Lat	0.25%	0.05%	0.40%
Bio × Ele × Lat	0.43%	0.28%	0.35%
1HF × Ele × Lat	**2.03%** **	**2.32%** **	**1.35%*** **
2HF × Bio × Est(Lat)	0.35%	0.29%	0.33%
2HF × 1HF × Est(Lat)	0.14%	0.27%	0.82%

2HF × Ele × Est(Lat)	**1.56%***	0.37%	**1.22%****
Bio × 1HF × Est(Lat)	**1.73%***	**1.84%***	**1.07%***
Bio × Ele × Est(Lat)	0.06%	0.42%	0.66%
1HF × Ele × Est(Lat)	**1.94%***	1.21%	**1.17%****
2HF × Bio × 1HF × Ele	0.01%	0.05%	0.23%
2HF × Bio × 1HF × Lat	0.21%	0.40%	0.33%
2HF × Bio × Ele × Lat	0.07%	0.25%	0.27%
2HF × 1HF × Ele × Lat	0.46%	0.48%	0.52%
Bio × 1HF × Ele × Lat	0.79%	0.40%	0.58%
2HF × Bio × 1HF × Est(Lat)	0.24%	0.55%	0.69%
2HF × Bio × Ele × Est(Lat)	0.24%	0.74%	0.79%
2HF × 1HF × Ele × Est(Lat)	**1.42%***	0.68%	0.63%
Bio × 1HF × Ele × Est(Lat)	**1.49%***	0.13%	0.33%
2HF × Bio × 1HF × Ele × Lat	0.19%	0.00%	0.39%
2HF × Bio × 1HF × Ele × Est(Lat)	0.47%	0.55%	0.20%

Figures

Figure 4.1 Spatial survey, effects of secondary habitat former across latitudes. Abundance (A, B, C) and richness (D, E, F) of invertebrates in northern (A, D), central (B, E) and southern (C, F) latitudes in absence or presence of primary (*Zostera muelleri* and seaweed alone) and secondary habitat former (seaweed entrained in *Zostera* bed). Seaweed species are represented mainly by *Ulva* sp. and *Gracilaria chilensis*. Sampling core = 0.0064 m^2. Error bars = 1 SE, n = 32. The test factors 'Estuary' and 'Elevation' were pooled. M = mud, Z = *Zostera*, S = seaweed, ZS = *Zostera* + seaweed. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'secondary habitat former' test factor, lower case letters to the 'primary habitat former' test factors.

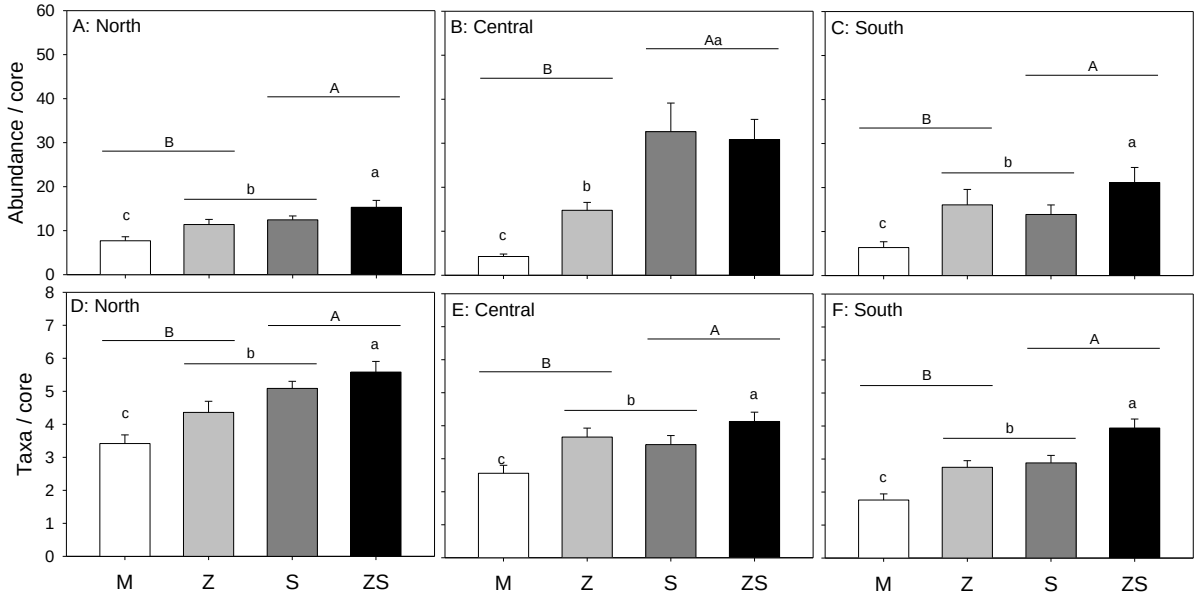


Figure 4.2 Spatial survey, effects of secondary habitat former across latitudes. nMDS plot of community structure (based on Bray-Curtis similarity on square root transformed data) in northern (A), central (B) and southern (C) latitudes in absence or presence of primary habitat former (*Zostera muelleri* and seaweed alone) and in absence or presence of secondary habitat former (seaweed entrained in *Zostera* bed). Seaweed species are represented mainly by *Ulva* sp. and *Gracilaria chilensis*. For simplicity, data were split into northern, central and southern latitude but results are from the same analysis and the three plots can be superimposed on each other (and therefore have the same taxa vectors). n = 32. The test factors 'Estuary' and 'Elevation' were pooled. M = mud, Z = *Zostera*, S = seaweed, ZS = *Zostera* + seaweed. Vectors were plotted for taxa contributing up to 50% of the multivariate community structure (1: *Micrelenchus tenebrosus*, 2: *Macomona liliana*, 3: *Austrovenus stutchburyi*, 4: *Zeacumantus subcarinatus*, 5: *Potamopyrgus estuarensis*, 6: errant polychaetes, 7: sedentaria polychaetes, 8: polychaetes tubes, 9: *Paphies australis*). Stress: 0.28.

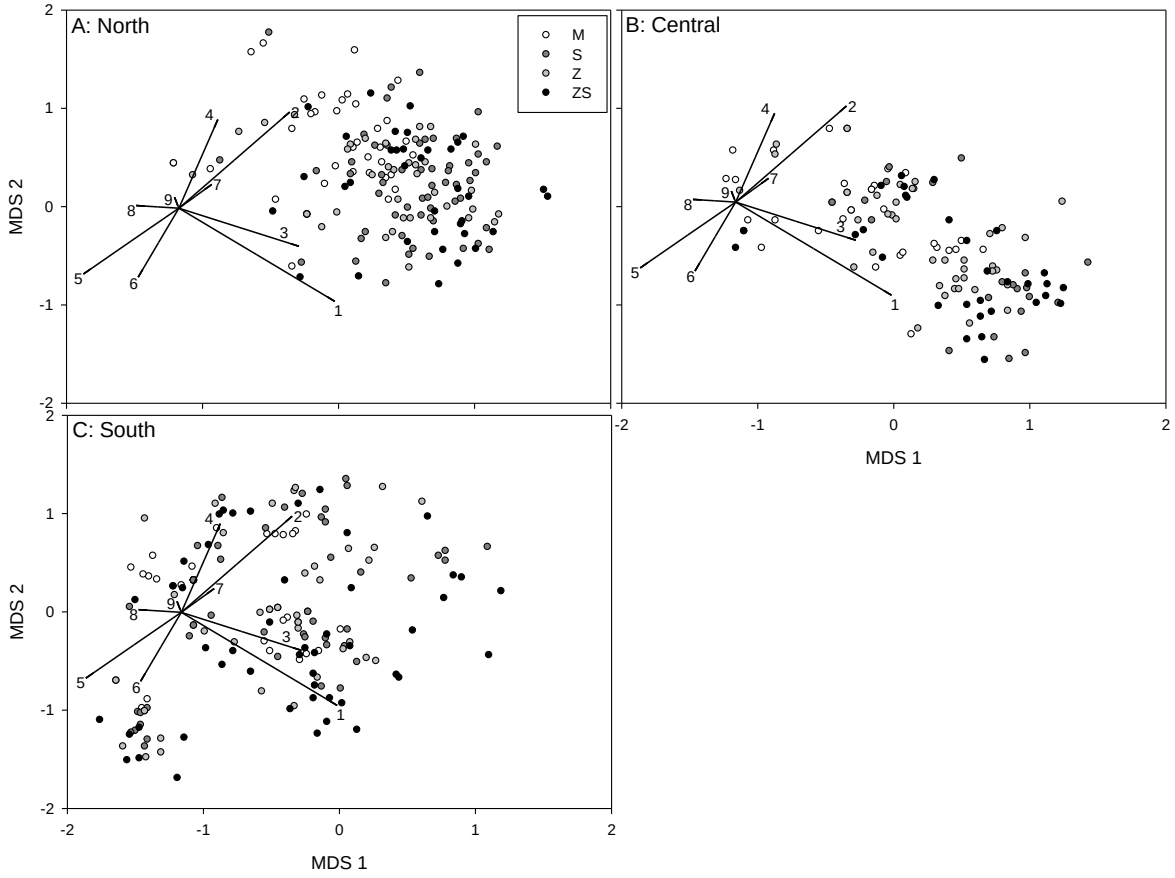


Figure 4.3 Seasonal survey, effects of secondary habitat former across seasons. Abundance (A, B) and richness (C, D) of invertebrates in summer (A, C) and winter (B, D) in absence or presence of primary habitat former (*Zostera muelleri* and *Ulva* sp. alone) and in absence or presence of secondary habitat former (*Ulva* sp. entrained in *Zostera* bed). Sampling core = 0.0064 m^2. Error bars = 1 SE, n = 32. The test factors 'Year', 'Site' and 'Elevation' were pooled. M = mud, Z = *Zostera*, U = *Ulva*, ZU = *Zostera* + *Ulva*. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refer to the 'secondary habitat former' test factor, lower case letters to the 'primary habitat former' test factors.

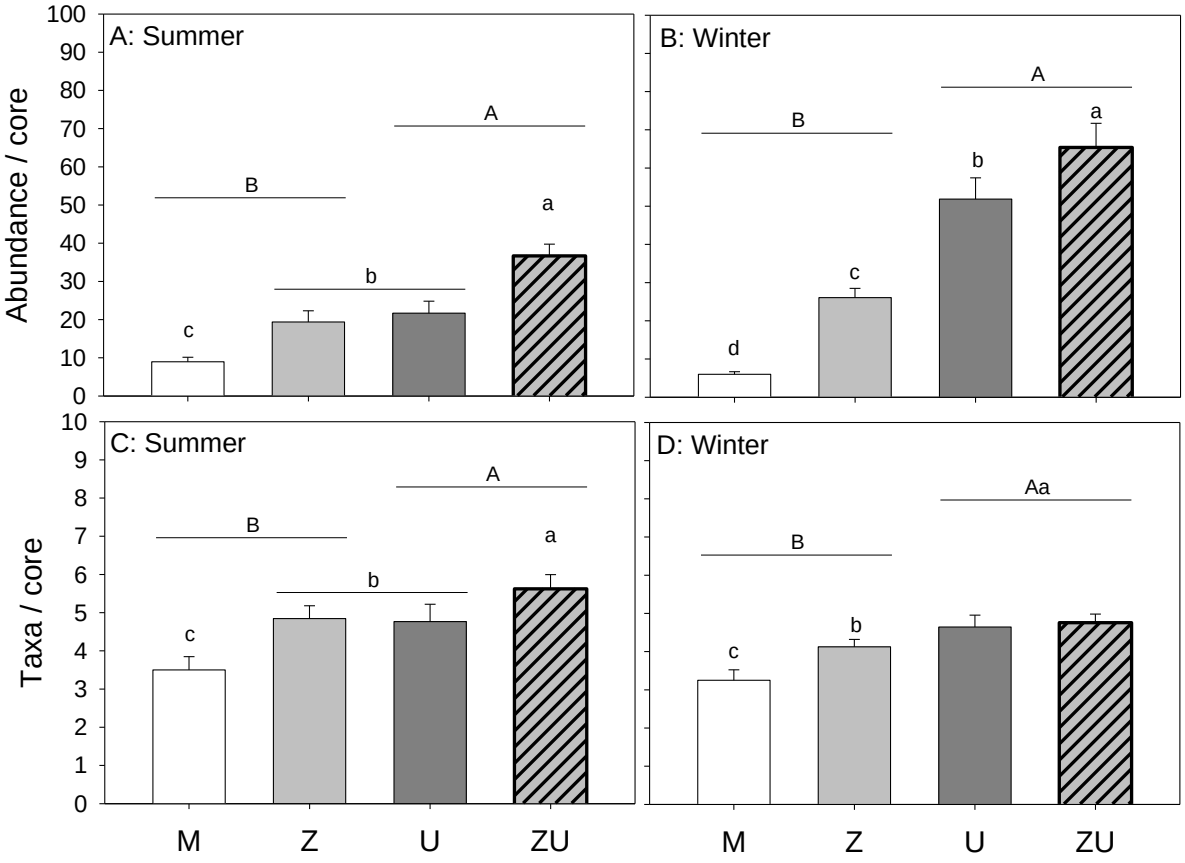


Figure 4.4 Seasonal survey, effects of secondary habitat former across seasons. nMDS plot of community structure (based on Bray-Curtis similarity on square root transformed data) in summer (A) and winter (B) in absence or presence of primary habitat former (*Zostera muelleri* and *Ulva* sp. alone) and in absence or presence of secondary habitat former (*Ulva* sp. entrained in *Zostera* bed). For simplicity, data were split into summer and winter but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). n = 32. The test factors 'Year', 'Site' and 'Elevation' were pooled. M = mud, Z = *Zostera*, U = *Ulva*, ZU = *Zostera* + *Ulva*. Vectors were plotted for taxa contributing up to 50% of the multivariate community structure (1: *Micrelenchus tenebrosus*, 2: *Austrovenus stutchburyi*, 3: errant polychaetes). Stress: 0.22.

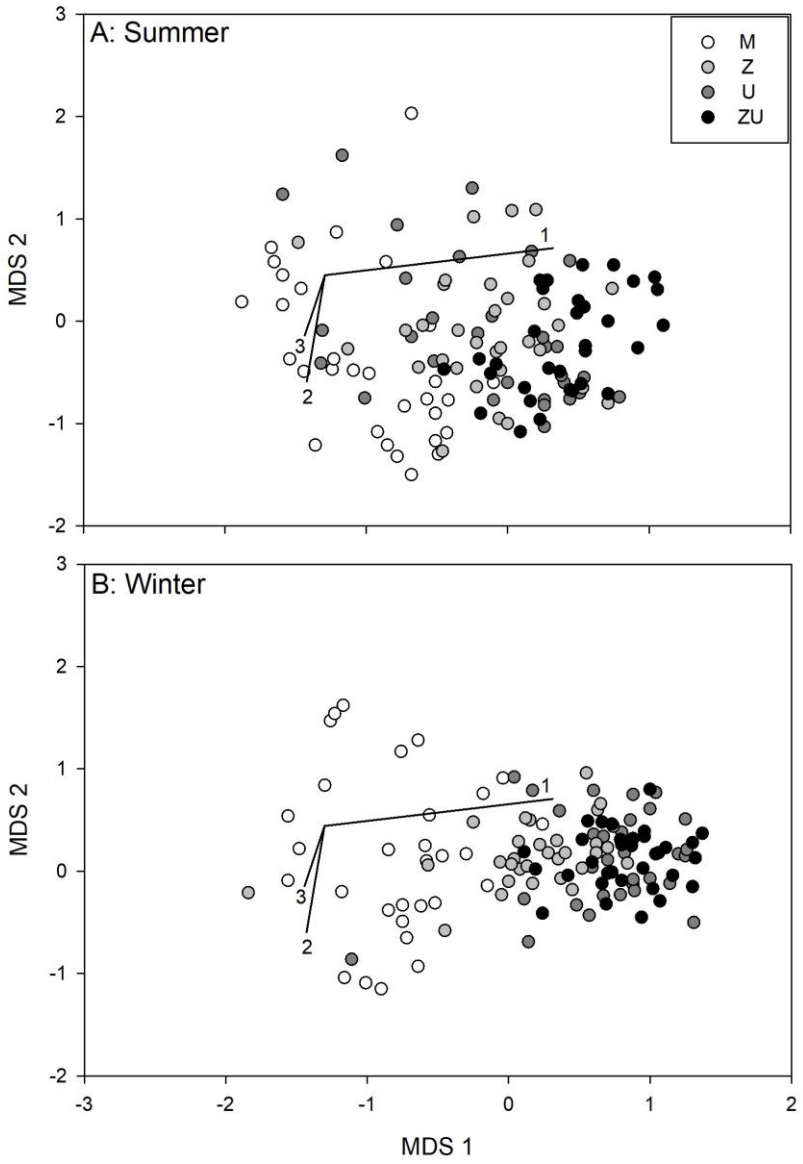


Figure 4.5 Field experiment 1, effects of secondary habitat former type and biomass. Abundance (A, B) and richness (C, D) of invertebrates in samples with no seaweeds (Z) and samples with living *Ulva* sp. (U) or mimic (M) in both low (L) and high (H) biomasses, in summer (A, C) and winter (B, D). Sampling core = 0.0064 m^2. The control treatment (Z, n = 8) was not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. Error bars = 1 SE, n = 8. The test factor 'Site' was pooled. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'secondary habitat former type' test factor, lower case letters to the 'secondary habitat former biomass' test factor.

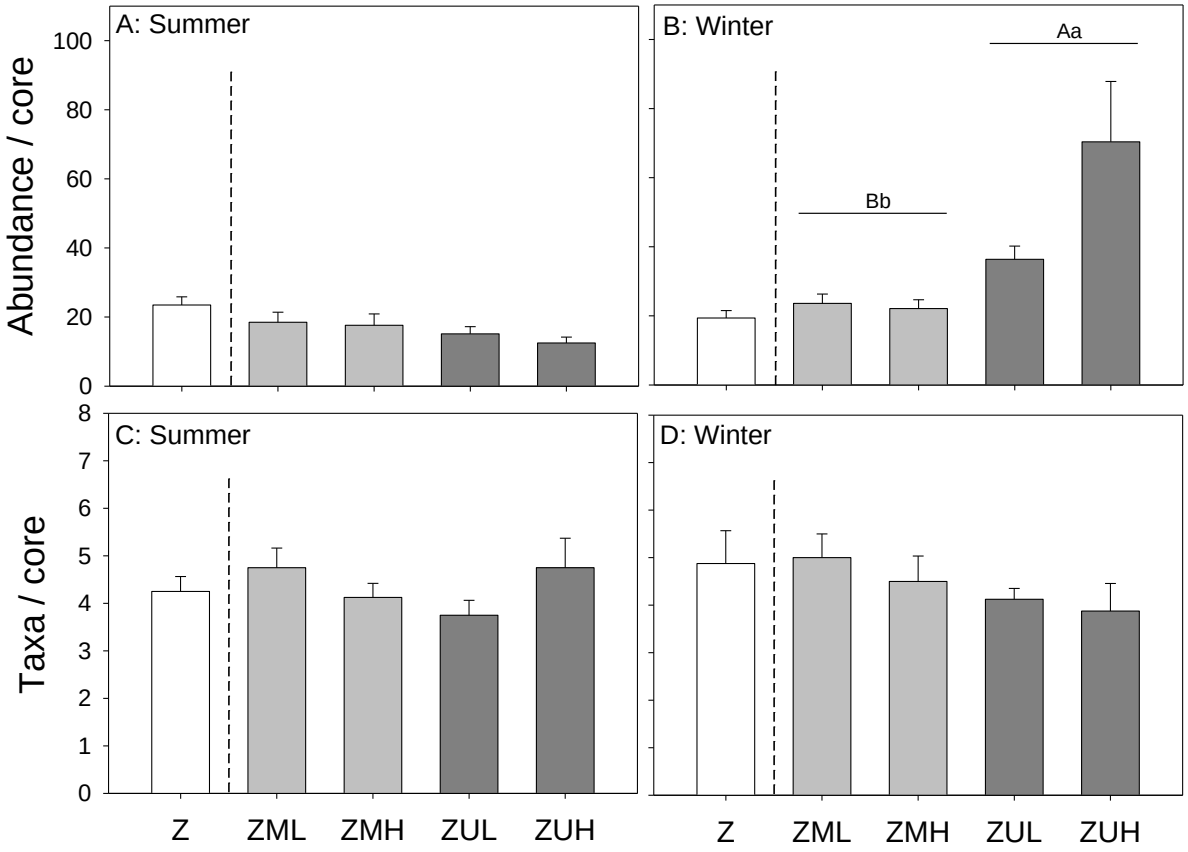


Figure 4.6 Field experiment 1, effects of secondary habitat former type and biomass. nMDS plot of community structure (based on Bray-Curtis similarity on square root transformed data) for samples with living *Ulva* sp. (U) or mimic (M) in both low (L) and high (H) biomass, in summer (A) and winter (B). The control treatment (Z, n = 8) was not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. For simplicity, data were split into summer and winter but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). n = 8. The test factor 'Site' was pooled. Vectors were plotted for taxa contributing up to 50% of the multivariate community structure (1: *Micrelenchus tenebrosus*, 2: *Diloma subrostrata*, 3: *Austrovenus stutchburyi*, 4: *Hemigrapsus crenulatus*). Stress: 0.21.

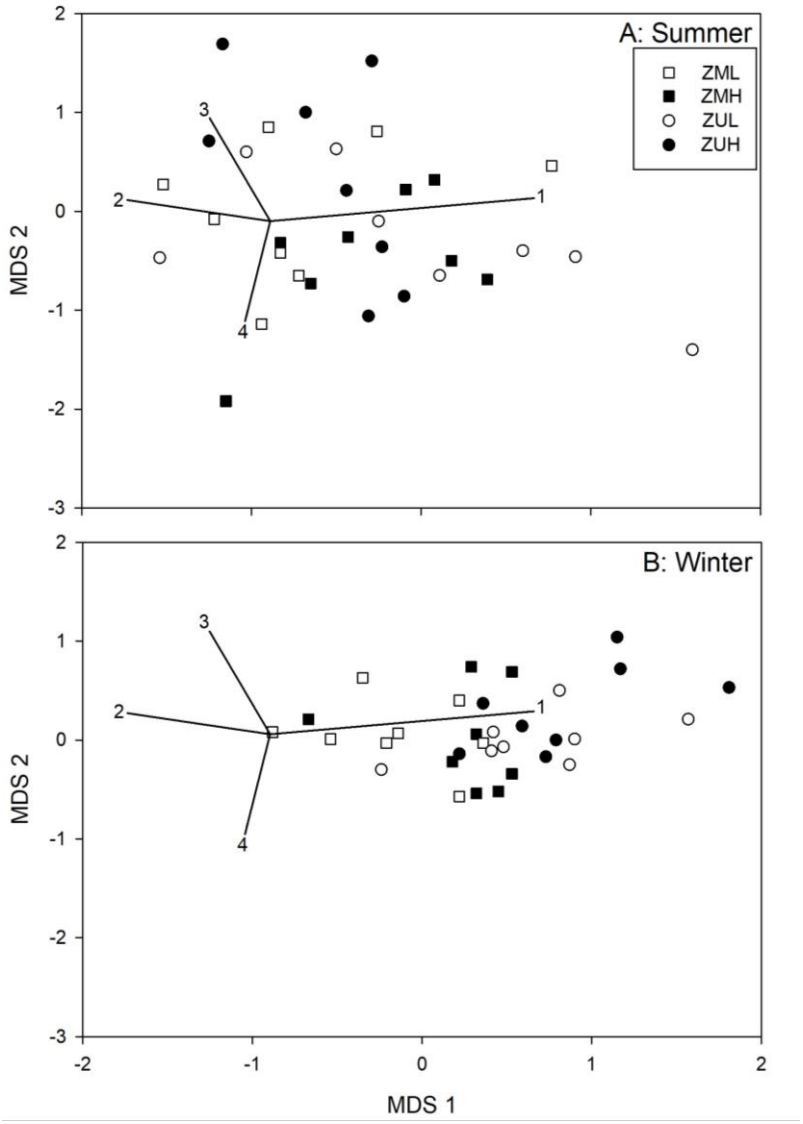


Figure 4.7 Field experiment 2, effects of secondary habitat formers morphology across latitudes. Abundance (A, B, C) and richness (D, E, F) of invertebrates in northern (A, D), central (B, E) and southern (C, F) latitudes in absence or presence of primary habitat former, *Zostera muelleri* (M vs Z, where M: mud, Z: *Zostera*), with two different mimics (Tw: twine; Ta: tape) in both low (L) and high (H) biomasses. Sampling core = 0.0064 m^2. The control treatments without secondary habitat formers (M, n = 12, and Z, n = 12) were not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. Error bars = 1 SE, n = 12. The test factors 'Estuary' and 'Elevation' were pooled. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'primary habitat former' test factor, lower case letters refer to the 'secondary habitat former' test factor.

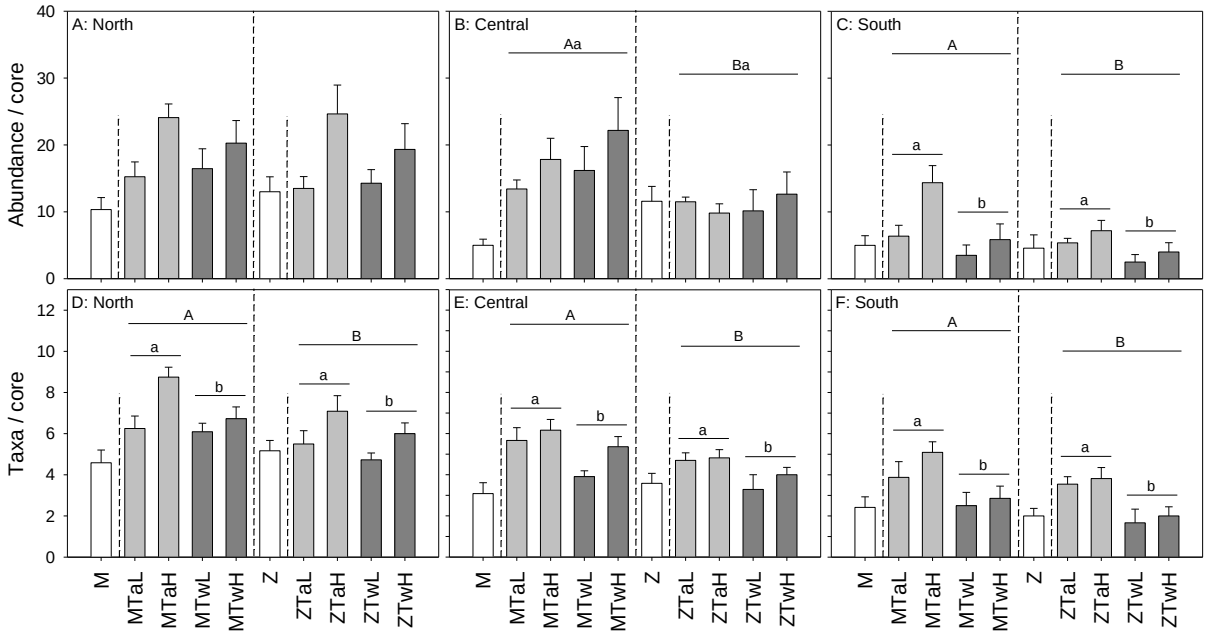


Figure 4.8 Field experiment 2, effects of secondary habitat formers morphology across latitudes. nMDS plot of community structure (based on Bray-Curtis similarity on square root transformed data) for samples in absence or presence of primary habitat former, *Zostera muelleri* (M vs Z, where M: mud, Z: *Zostera*), with two different mimics (Tw: twine; Ta: tape) in both low (L) and high (H) biomasses, in northern (A), central (B) and southern (C) latitudes. The control treatments without secondary habitat formers (M, n = 12, and Z, n = 12) were not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. For simplicity, data was split into northern, central and southern latitudes but results are from the same analysis and the three plots can be superimposed on each other (and therefore have the same taxa vectors). n = 12. The test factors 'Estuary' and 'Elevation' were pooled. Vectors were plotted for taxa contributing up to 50% of the multivariate community structure (1: *Micrelenchus tenebrosus*, 2: errant polychaetes, 3: *Spisula aequilatera*, 4: *Zeacumantus subcarinatus*, 5: *Hemigrapsus crenulatus*, 6: *Diloma subrostrata*, 7: polychaete tubes, 8: *Austrovenus stutchburyi*, 9: amphipods, 10: *Macomona liliana*). Stress: 0.27.

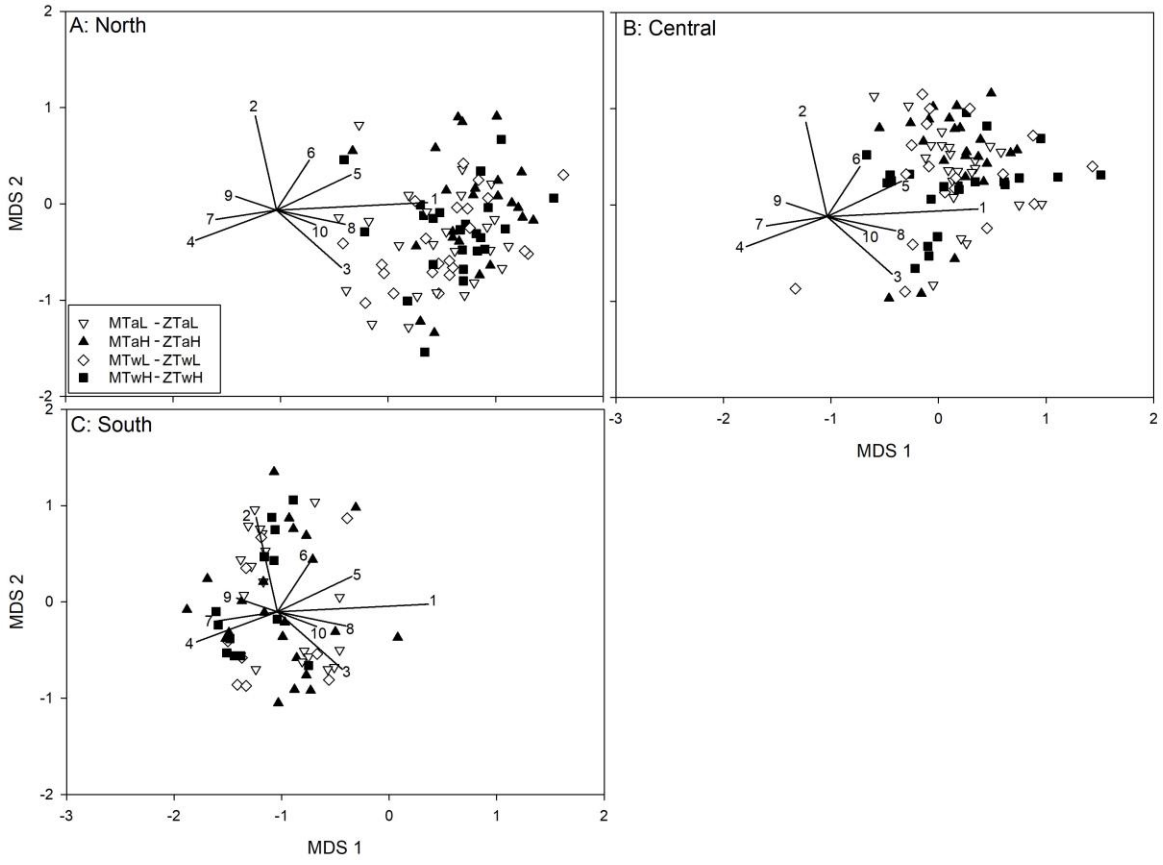


Figure 4.9 Field experiment 3, effect of predators. Habitat occupancy of the gastropod *Micrelenchus tenebrosus* with (+) and without (-) presence of a *Hemigrapsus crenulatus* crab. Only 3.2% of all snails exposed to predatory crabs were consumed. Gastropods were counted as attached to either mud (M), *Ulva* sp. (U). or *Zostera muelleri* (Z). n = 6. The test factor 'Biomass' was pooled.

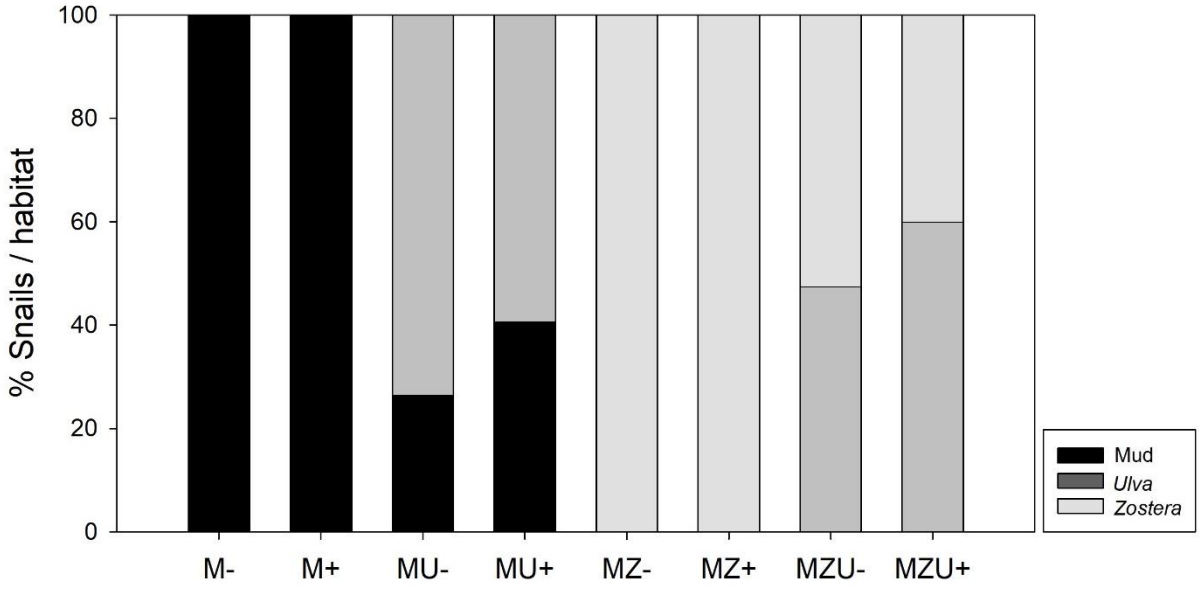


Figure 4.10 PCO analysis of morphological traits of living (circles) or mimics (squares) of primary (white: *Zostera muelleri*) and secondary (black: *Gracilaria chilensis*; grey: *Ulva* sp.) habitat formers. n = 10. SDw: surface area:dry; Db: fractal dimension; C: circularity; Λ: lacunarity. Data were square-rooted and normalised prior to analysis.

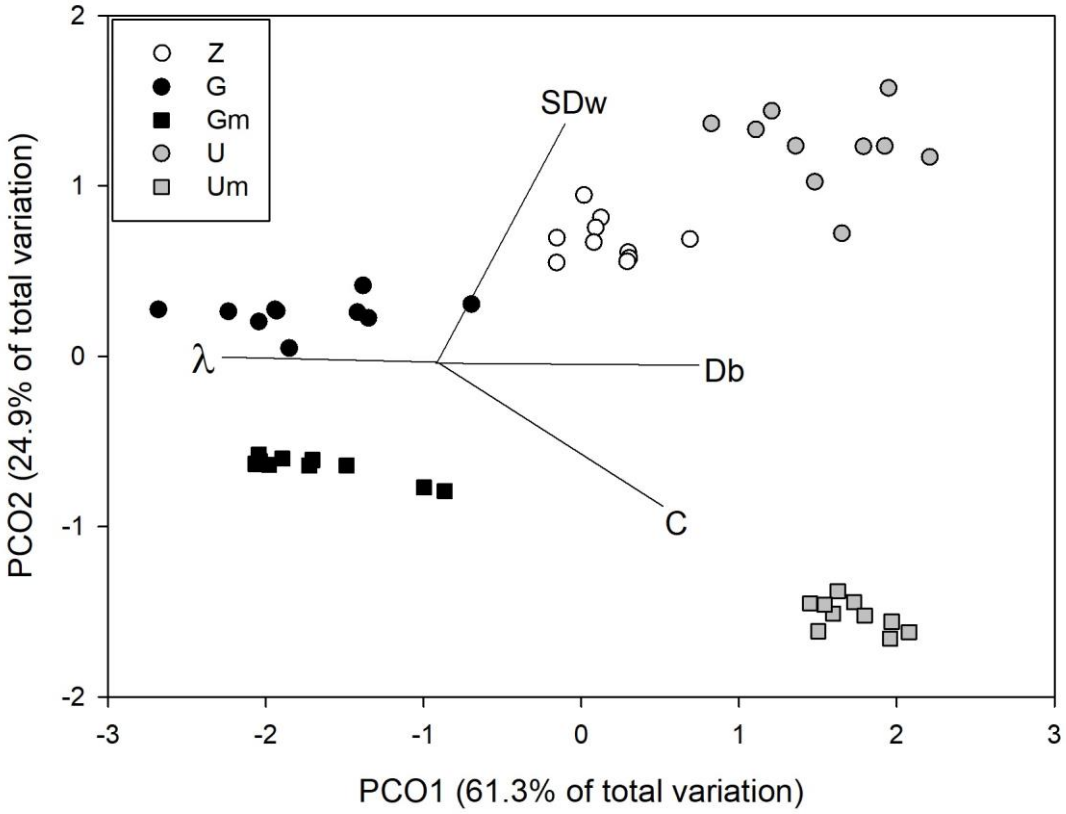


Figure 4.11 Morphological traits of primary habitat former (Z: *Zostera muelleri*) and the secondary habitat formers (U: *Ulva* sp., G: *Gracilaria chilensis*, Um: *Ulva* mimic, Gm: *Gracilaria* mimic). Error bars 1 SE, n = 10. In most of cases, error bars are too small to be visible. Different letters indicate significant differences as detected by pair-wise t-test comparisons.

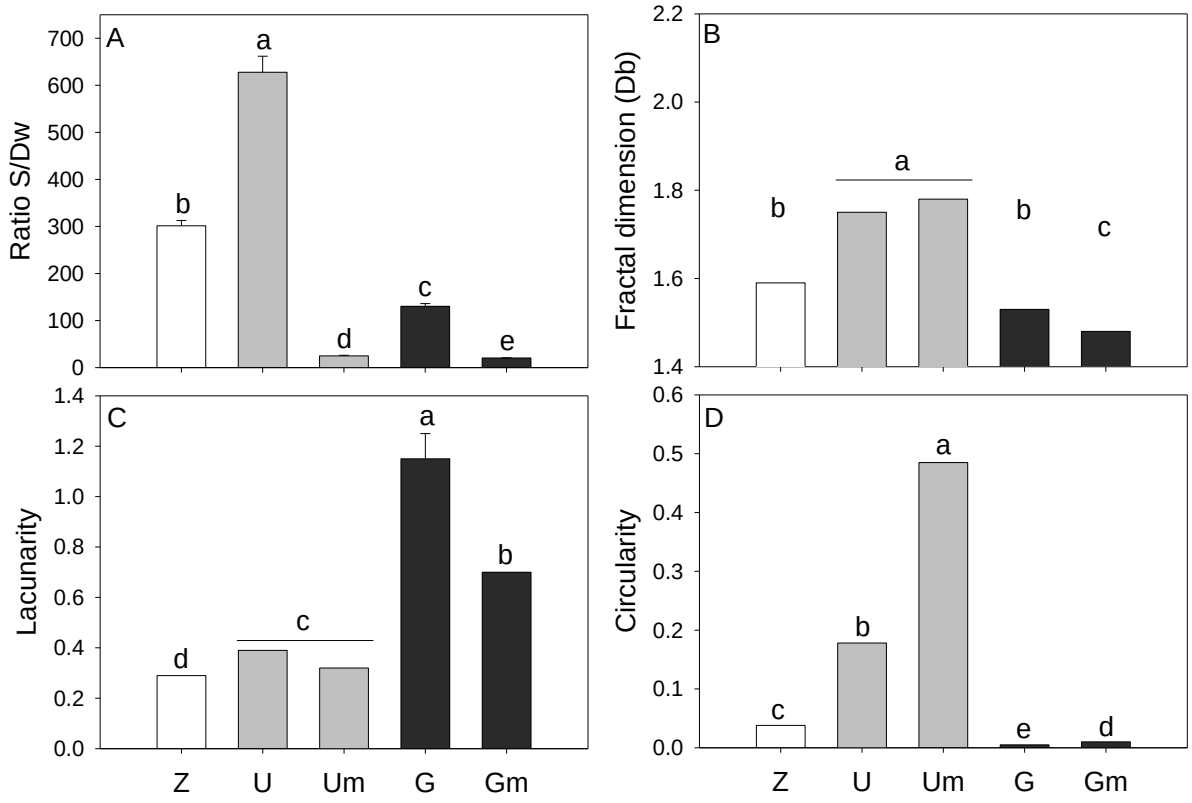
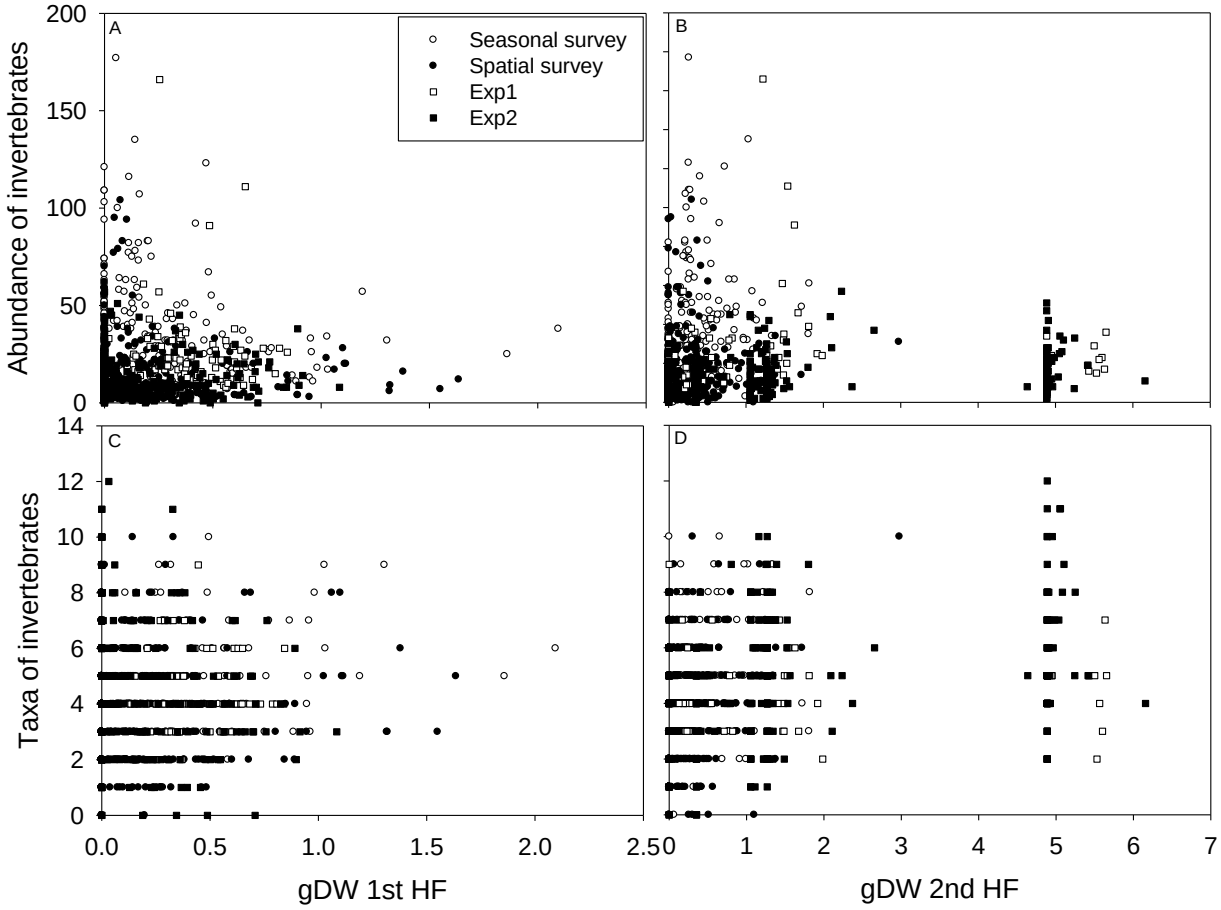


Figure 4.12 Correlation between the biomass of primary habitat former (*Zostera muelleri*; A, C), the secondary habitat former (the seaweeds *Ulva* sp., *Gracilaria chilensis*, *Lophothamnion hirtum*, *Polysiphonia* sp.; B, D) in relation to the abundance (A, B) and the taxonomic richness (C, D) of invertebrates. Number of cores collected = 446. 257, 80 and 360 for the spatial survey, seasonal survey, experiment 1 and experiment 2, respectively. A few data outliers were removed for visual clarity: 14.59 gDW vs 19 invertebrates and 14.59 gDW vs 8 taxa (both from experiment 2). Spearman's rank correlation analysis: A, $r_{Spearman} = 0.10$, $p = 0.003$; B, $r_{Spearman} = 0.18$, $p = 0.001$; C, $r_{Spearman} = -0.01$, $p = 0.7$; D, $r_{Spearman} = 0.27$, $p = 0.001$.



CHAPTER 5: Effects of local anthropogenic stressors on a habitat cascade in an estuarine seagrass system

5.1 ABSTRACT

Recent research has shown that co-occurring primary and secondary habitat-forming species typically support higher biodiversity than monocultures of the primary habitat former alone. However, these 'habitat cascades' may not be universal and, from a conservation perspective, it is important to know if, when and where positive effects on biodiversity change to negative effects. Here I tested how the common anthropogenic stressors, fertilization and sedimentation, and unattached secondary habitat-forming *Ulva* seaweeds affected the primary habitat-forming seagrass, *Zostera muelleri*, and its associated invertebrates in the Avon-Heathcote Estuary, in New Zealand. I experimentally stressed *Zostera*, adding different fertilization and sediment levels in a 4×4 factorial design. Fertilization had little impact whereas even low sedimentation levels had strong negative effects on *Zostera* and its associated fauna. In a second experiment sediments and *Ulva* were added in a 2×2 factorial design to seagrass beds and unvegetated mudflats to test if sediment stress modifies habitat cascades. The experiment was repeated two times at two elevation levels to test if results were consistent in space and time. I found strong negative effects of sediments, irrespective of spatio-temporal conditions, and that negative effects of sediments on invertebrate abundances were elevated in presence of the secondary habitat former. These results provide experimental evidence that a strong anthropogenic stressor can destabilize a habitat cascade and highlight the importance of these interactions in estuarine ecosystems characterized by low biodiversity and stressful environmental conditions.

5.2 INTRODUCTION

There is accumulating evidence that co-occurring primary and secondary habitat-forming species typically support higher biodiversity than monocultures of the primary habitat-forming species alone (Altieri et al. 2007, Bishop et al. 2012, Thomsen et al. 2010). However, these 'habitat cascades' may not be universal and, from scientific and conservation perspectives, it is important to know if, when and where positive effects on biodiversity switch to negative effects. For example, habitat cascades could break down if secondary habitat formers outcompete primary habitat formers or if environmental stressors negatively affect the primary and/or secondary habitat formers. Despite the growing literature documenting a positive net effect of secondary habitat-forming species on biodiversity (Thomsen et al. 2010), I am not

aware of studies that have experimentally tested if or how stressors may destabilize habitat cascades.

Habitat cascades are prolific in seagrass beds as epiphytes attach to (Bologna and Heck 1999, Gartner et al. 2013, Hall and Bell 1988), drift algae entangle around (Holmquist 1997, Thomsen 2010, Thomsen et al. 2013) and molluscs embed among (Thomsen et al. 2013, Valentine and Heck Jr 1993) seagrass leaves. Seagrasses provide habitat for secondary habitat-forming species, but they also stabilize sediments, attenuate waves, and sequester carbon (Connolly 1997, Currás et al. 1994) and, importantly, increase the abundance and diversity of seagrass-associated fauna (Abele 1974, Boström and Bonsdorff 1997, Hall and Bell 1988, Heck Jr and Orth 1980, Heck et al. 1995, Kohn 1967, Stoner and Lewis 1985).

All of these ecosystem functions are susceptible to anthropogenic stressors, as evidenced by the rapid decline in seagrass beds around the world (Orth et al. 2006, Short et al. 2011, Waycott et al. 2009). Key human activities that threaten seagrasses include global stressors like climate change (Diaz-Almela et al. 2007, Ehlers et al. 2008) and invasive species (Williams 2007) as well as local stressors such as nutrient pollution and increased sediment loads (Barbier et al. 2011, Orth et al. 2006, Short et al. 2011, Waycott et al. 2009). These stressors typically co-occur (Burkholder et al. 1992, Crain et al. 2008, Halpern et al. 2008) and it is therefore important to understand direct, indirect and interactive effects on the seagrass themselves and on associated invertebrates (McGlathery 2001, Thrush et al. 2004, Wernberg et al. 2012). It is reasonably well understood how fertilization or sedimentation affect seagrasses in isolation (Burkepile and Hay 2006, Cabaço et al. 2008) but it is less known how these stressors interact, if interactions are dose-dependent and how dose-dependency may affect seagrass-associated invertebrates. Furthermore, excessive amounts of nutrients typically stimulate growth of seaweeds inhabiting seagrass beds, thereby favouring epiphytes and drift seaweeds over the seagrasses themselves (Pedersen and Borum 1996, Sand-Jensen and Borum 1991). Nutrient-fuelled rapid growth of epiphytes and drift seaweeds can shade seagrass and cause benthic anoxia (due to respiration and decomposition) below the canopy, and thereby stress seagrasses (Cambridge and McComb 1984, Holmer and Bondgaard 2001, Thomsen et al. 2012b). Thus, it is possible that epiphytes and drift seaweeds can both increase and decrease habitat quality for seagrass-associated invertebrates, depending on other environmental stressors, like nutrient and sediment levels. However, I am not aware of any studies that have tested how the ecological importance of seaweeds within seagrass beds may change from positive or neutral to negative depending on the environmental context.

I addressed these research gaps by testing if (i) impacts of nutrients and sediments on seagrass performance and seagrass-associated invertebrates are dose-dependent and interactive, and (ii) sediment stress affects the strength and direction of how drift seaweeds affect seagrass and their associated invertebrates (that is, if sediments modify the strength of habitat cascades). These hypotheses were tested with two experiments in the Avon-Heathcote Estuary, in Christchurch, New Zealand. In this system, the primary habitat-forming species is the seagrass *Zostera muelleri*, the only seagrass species in New Zealand (Short et al. 2007). It is relatively common on sandy substrates and in estuaries throughout New Zealand and temperate Australia (Den Hartog 1970), where it modifies sediment deposition, stabilizes substrate, and provides habitat for drift seaweeds and invertebrates (Connolly 1994a, Connolly 1994b, Ferrell and Bell 1991, Fonseca et al. 2011). The secondary habitat-forming seaweed species here were sheet-forming *Ulva* spp. (dominated by *U. curvata*), that can form dense mats in sedimentary estuaries in New Zealand (Jones et al. 2005, Marsden and Maclaren 2010, Marsden and Bressington 2009) and worldwide (Fletcher 1996).

5.3 MATERIALS AND METHODS

Study sites were located in the Avon-Heathcote Estuary (43°33'11.7"S, 172°44'39.4"E), where the seagrass *Zostera muelleri* and the seaweeds *Ulva* sp. (hereafter *Zostera* and *Ulva*, respectively) are common. The Avon-Heathcote Estuary is bordered by Christchurch and freshwater enters from the Avon (north) and Heathcote (south-west) rivers (McClatchie et al. 1982). The estuary is ca 8 km^2 and is predominantly intertidal, with a tidal range of 2.2 m at spring tides and 1.7 m at neap tides (Findlay and Kirk 1988). During high tide, the maximum depth is 5.5 m in the deepest channel (Webb 1972) while during low tide 85% of the estuary is characterized by intertidal mudflat (Hollever and Bolton-Ritchie 2016). The study area was located in the eastern part of the estuary, close to the Brighton Spit, between Tern and Plover streets.

5.3.1 Experiment 1: interactive effects of eutrophication and sedimentation

The first experiment tested the hypothesis that there are interactive effects of sediment and nutrient stress on seagrass performance and seagrass-associated invertebrates. More specifically, I tested for interactive effects between four sediment and four fertilization levels on *Zostera* biomass and shoot density, and on invertebrate abundance, richness and community structure.

I established 25×25 cm plots in an intertidal seagrass bed. Prior to experimental manipulations, shoot density was counted in each plot centre within a 10×10 cm quadrat. Sedimentation was manipulated by adding 0 (control), 1, 2 or 4 cm of sediments, corresponding to sediment levels added in many other seagrass-sediment stress experiments (Cabaço and Santos 2007). Sediments were collected from an adjacent mudflat and sieved using a 1-cm sieve to remove macroinvertebrates, shells, stones and seaweeds. Sediments were added to plots by slowly drizzling the unconsolidated sieved sediment over each plot until the required depth was reached (as in Airoldi and Virgilio 1998). Fertilization was manipulated by inserting 0, 2, 4, or 8 Jobes Fertilizer Spikes (13% nitrogen, 4% phosphate and 5% potash, corresponding to 0.16 gN, 0.05 gP and 0.06 gK per spike) into the sediments within the plots, in a fully crossed design. Each treatment combination was replicated 3 times. These nutrient levels and methods are common for fertilization experiments in seagrass beds (Burkepile and Hay 2006, Worm et al. 2000). The experiment was run in the summer growing season in February-March 2016 over four weeks. Sediment levels were maintained every five days by adding new sediments (if they were eroded away). Fertilizer was re-applied after two weeks, corresponding to a total addition of 2.56 gN m^{-2} and 0.79 gP m^{-2} for the lowest application and 10.23 gN m^{-2} and 3.15 gP m^{-2} for the highest application level. Three days before the experiment ended, a 10 cm silver stick was inserted 4 cm into the sediment (1.2 mm diameter, 99% Ag) in the centre of each plot to measure the depth of the sulphide layer in the sediment, as a proxy for oxygen penetration (as in Holmer et al. 2009, Holmer et al. 2011, Thomsen et al. 2012b). At the end of the experiment, silver sticks were collected first and then sediment cores were collected from each plot center (a circular 9 cm inner diameter = 0.0064 m^2 core pushed 10 cm down into the sediment). Each collected core was washed in the field in 1-mm mesh bag to retain seagrass, seaweeds and fauna before being transported to the laboratory for processing.

5.3.2 Experiment 2: effects of sedimentation on the habitat cascade

The second experiment tested if sedimentation destabilizes seagrass-seaweed habitat cascades. More specifically, I tested if addition of sediments affects invertebrate communities, and whether these effects are influenced by seaweeds, elevation levels, and seasons. This experiment had the following design: 2 levels of seagrass (± 1st HF, Mud vs *Zostera*) × 2 levels of *Ulva* (± 2nd HF, Mud vs *Ulva*) × 2 sedimentation levels (± addition of sediments) × 2 elevation levels (intertidal vs shallow subtidal) × 2 seasons (summer vs winter) × 3 replicates. Sediments and fronds of *Ulva* were collected from the study site. Sediments were sieved as in the previous experiment and *Ulva* fronds were rinsed and shaken to remove

macroinvertebrates. Again, 25×25 cm plots were established in both a seagrass bed and on an adjacent mudflat. Shoot density was estimated as in the previous experiment, before 2.8 gWW of *Ulva* was added around the seagrass leaves by pegging them flush into the sediment with 2 u-bent 20 cm metal pegs. Pegs were also added to the control plots to avoid confounding treatments by the presence of pegs. Finally, 1 cm of sediments was added to the 'sedimentation' treatments, using similar methods as in the previous experiment (the lowest level applied in experiment 1 that still had an adverse effect on seagrass; see Results section). The experiment ran for two weeks in July and the entire experiment was repeated in November 2016. Maintenance was done every five days, adding new sediments and new *Ulva* fronds where necessary (*Ulva* only had to be re-applied to plots without sediments). Three days before the experiment was terminated, sulphide oxidation was measured with silver sticks and cores were collected as described in the previous experiment. Note that *Ulva* in this experiment can be considered to be both a primary and secondary habitat former, depending on whether it was collected from the mudflat or from the seagrass bed (Edgar and Robertson 1992, Thomsen et al. 2012a, Thomsen et al. 2013). Finally, I also note that both 'Season' and 'Elevation' technically are 'unreplicated' test factors (Hurlbert 1984) because I only included one summer, one winter, one subtidal and one intertidal experiment. My aim here was primarily to test if the effect of *Ulva* is consistent in space and time and references to 'seasonal' and 'elevational' effects are therefore of less importance (still, I include, by design, a cold and a warm month and subtidal and intertidal elevations, to cover a wide range of ambient abiotic conditions, and both test factors were therefore treated as fixed in statistical analyses).

5.3.3 Laboratory analysis

In the laboratory, core samples were rinsed onto a 1-mm sieve to retain macroinvertebrates, seagrass and seaweeds. Seaweed and seagrass (split to leaves and roots) were weighed after drying at 55°C for 48 h or until no further weight loss could be detected. All invertebrates were counted and identified to operational taxonomic units (conspicuous taxa to species levels, small inconspicuous taxa to Order or Family) with a dissecting microscope at 40× magnification, and preserved in 70% ethanol. Silver sticks were processed by measuring the distance to the blackened part with a digital caliper (blackening is a result of reduction of Ag to Ag_2S).

5.3.4 Statistical analysis

I tested for effects of fertilization and addition of sediment and macroalgae on (i) distance of blackened silver sticks, (ii) seagrass shoot density, (iii) seagrass above-ground biomass, (iv)

total invertebrate abundance, (v) invertebrate taxonomic richness, and (vi) invertebrate multivariate community structure. Invertebrate counts were square-root transformed to reduce the statistical importance of a few highly dominant taxa and to decrease variances for the most abundance taxa. Responses were analyzed with permutational-based factorial analysis of variance (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. All factors were treated as fixed. Results were considered significant if $p < 0.05$. Significant results for test factors with more than two levels were followed by post-hoc pair-wise t-tests. Finally, the biomass of *Zostera* and *Ulva* were correlated against total invertebrate abundance and richness, using Spearmans' rank correlation coefficient on all samples from the two experiments with and without sediment stress (fertilized samples were classified as 'unstressed' because nutrients did not inhibit seagrass or invertebrates; see Results section).

5.4 RESULTS

5.4.1 Experiment 1: effects of nutrients and sedimentation

Silver sticks and seagrass. There was no difference in the depth of the oxidation layer across the treatments (Table 5.1, Fig. 5.1A). However, there were significant negative effects of sedimentation (S) on both leaf biomass and shoot density ($p = 0.001$, Table 5.1; $\eta^2 = SS_{Explained}/SS_{Total}$; $\eta^2 = 86.9\%$ and 89.3%, respectively), but no effects of added fertilizers (F). Post-hoc pair-wise comparisons showed, as expected, that the highest seagrass leaf biomass and shoot densities were in control plots, intermediate levels in treatments with 1 cm of sediment and lowest in treatments with 2 and 4 cm of sediments ($S_0 > S_1 \geq S_4 \geq S_2$, Fig. 5.1B; $S_0 > S_1 > S_2 = S_4$, Fig. 5.1C).

Invertebrate abundance. I found 350 invertebrates representing 12 taxa in the 48 samples. The most important taxa were *Austrovenus stutchburyi* (194 individuals), juvenile crabs (33) and the trochids *Diloma subrostrata* (24) and *Micrelenchus tenebrosus* (19).

Invertebrate abundance was significantly affected only by sedimentation (Table 5.1, Fig. 5.1D), with highest abundances in the control plots (12.50 ± 1.00 ind. core^{-1}), intermediate abundances at 1 and 2 cm treatments (6.75 ± 1.05 and 5.75 ± 0.93) and lowest abundances in 4 cm treatments (4.17 ± 0.73) ($S_0 > S_1 = S_2 > S_4$, Fig. 5.1D).

Invertebrate richness. There was a highly significant Fertilization × Sedimentation interaction on invertebrate richness ($p = 0.001$, $\eta^2 = 32.9\%$, Table 5.1). This demonstrated that although sedimentation generally had a negative effect on richness (see below), the effect was stronger at the highest fertilization level (Fig. 5.1E). Irrespective of this interaction effect, sedimentation also had a highly significant single factor effect on richness ($p = 0.001$, $\eta^2 = 38.7\%$, Fig. 5.1E), with more taxa in the control plots (4.58 ± 0.29 taxa core^{-1}) compared to any of the other sediment treatments (2.92 ± 0.29, 2.75 ± 0.37 and 2.42 ± 0.29) ($S_0 > S_1 = S_2 = S_4$, Fig. 5.1E).

Invertebrate community structure. As expected, sedimentation also had a significant effect on multivariate community structure ($p = 0.01$, $\eta^2 = 14.2\%$, Table 5.1) but there were no effects of fertilization or the Sedimentation × Fertilization interaction. The MDS ordination showed a moderate separation between the unstressed control plots and the sediment stressed plots ($S_0 \neq S_1 = S_2 = S_4$, Fig. 5.2). Only two taxa, *Austrovenus stutchburyi* and small crabs, accounted for 50% of the variability in the MDS plots, with their abundance vectors pointing toward the unstressed control plots (Fig. 5.2).

5.4.2 Experiment 2: effects of sedimentation and drift alga

Silver sticks and seagrass. There was no difference in the depth of the oxidation layer across the treatments (Table 5.1, Fig. 5.3A-B). The biomass of seagrass leaves was strongly affected both by the Sedimentation × Season interaction ($p = 0.001$, $\eta^2 = 16.2\%$) and the two single test factors (Sedimentation: $p = 0.001$, $\eta^2 = 51.2\%$; Season: $p = 0.001$, $\eta^2 = 11.4\%$). More specifically, there was a strong negative effect of sediments on seagrass leaves, reducing biomass from 0.21 ± 0.04 to 0.07 ± 0.01 gDW core^{-1} (Fig. 5.3C-D), although this effect was stronger in November than July (cf. the significant Sedimentation × Season interaction). Seagrass shoot density was also significantly affected by the Sedimentation × Season interaction ($p = 0.001$, $\eta^2 = 21.1\%$), with stronger negative effects in November (Fig. 5.3E). In addition, there was a strong negative single-factor effect of sedimentation ($p = 0.001$, $\eta^2 = 65.1\%$), reducing densities from 300.6 ± 29.82 to 63.8 ± 7.64 shoots m^{-2} (Fig. 5.3E-F), and a less important, but still significant, effect of the secondary habitat former ($p < 0.05$, $\eta^2 = 1.6\%$), where *Ulva* reduced shoot density from 197.69 ± 35.63 to 149.86 ± 28.13 shoots m^{-2} (Fig. 5.3E-F).

Invertebrate abundance. A total of 1,036 invertebrates, representing 13 taxa, were counted in the 96 samples. The most abundant were *Austrovenus stutchburyi* (517 individuals), *Micrelenchus tenebrosus* (222), errant polychaetes (73), *Diloma subrostrata* (73) and the bivalve *Macomona liliana* (41).

Statistical results were complex, with 7 significant interaction effects (e.g., 1st HF × Sedimentation, Sedimentation × Elevation, Sedimentation × Season, Table 5.1). However, most of these effects explained only a small proportion of the total sum of squares of the Anova model ($\eta^2 < 7\%$ for each interaction). Furthermore, these interactions reflected relatively 'easy-to-interpret' interactions, demonstrating that the magnitude of sediment effects was slightly modified by environmental context (e.g., as in Experiment 1, with a stronger negative effect of sediment in November compared to July, Fig. 5.3G-H). The single most important significant test factor was, as in Experiment 1, a negative effect of sedimentation ($p = 0.001$, $\eta^2 > 35\%$, Table 5.1), which reduced abundances from 15.38 ± 1.18 ind. core^{-1} to 6.21 ± 0.50 (Fig. 5.3G-H). As expected, invertebrate abundance was also affected by Season, with higher densities in November (12.27 ± 1.26) compared to July (9.31 ± 0.92). Finally, there was a positive net effect of adding *Ulva* to seagrass in the July samples without sediment stress, but this effect was reversed in treatments with added sediments (Fig. 5.3G-H).

Invertebrate richness. There were three significant interaction effects, in concert accounting for 10% of data variability. Again, Sedimentation was by far the most important significant test factor ($p < 0.001$, $\eta^2 = 39.2\%$, Table 5.1). Sedimentation decreased the number of taxa from 4.46 ± 0.20 taxa core^{-1} to 2.40 ± 0.17, but in contrast to the abundance data I found no effects of season or adding *Ulva* to *Zostera* beds in either November or July (Fig. 5.3I-J).

Invertebrate community structure. A multivariate analysis of community structure showed 8 significant interactions, including a 4-factor interaction. However, all of these interactions accounted for little of the data variability ($\eta^2 < 3\%$ for each interaction, Table 5.1). Again, sediment addition alone accounted for most variability ($\eta^2 = 13.2\%$) and, as for Experiment 1, the communities in control plots were different from those in the sediment treatments ($S_0 \neq S_1$, Fig. 5.4). Fifty percent of the multivariate community structure was explained by six species, but mostly by *Micrelenchus tenebrosus* and *Diloma subrostrata*, correlating positively with unstressed control plots in the presence of biogenic habitat formers (i.e., with both *Zostera* and *Ulva*, Fig. 5.4).

5.4.3 Correlations

For the unstressed samples, invertebrate abundances ($r_{Spearman} = 0.36$, $p = 0.005$, Fig. 5.5A) and richness ($r_{Spearman} = 0.28$, $p = 0.03$, Fig. 5.5B) correlated positively with the biomass of *Zostera*, but not *Ulva* ($p > 0.05$, Fig. 5.5C-D). No significant correlations were found for stressed samples ($p > 0.05$, Fig. 5.5).

5.5 DISCUSSION

Here I demonstrated strong negative effects of sedimentation on seagrass performance and on seagrass-associated invertebrates. I also documented a habitat cascade where drifting seaweeds functioned as secondary habitat formers. This habitat cascade broke down when sediments were added to the seagrass bed, reversing the effects of seaweeds on invertebrates from positive or neutral to negative effects, a pattern that was stronger in the warm than cold experimental month. The main reason of this reversed effect is probably attributable to the mechanical effect of sedimentation on the tridimensional structure of the secondary habitat former which, collapsing, is not able to provide beneficial effects. These results provide an experimental demonstration of how habitat cascades, which normally enhance biodiversity, can have negative effects on biodiversity under high stress levels.

5.5.1 Effects on seagrass

Seagrass performance was not affected by synergistic interactions between fertilization and sedimentation. Synergistic effects have often been assumed to be common when multiple stressors co-occur (Myers 1995, Sala et al. 2000) but empirical evidence has shown that this may not always be the case (Crain et al. 2008, Darling and Côté 2008). Here the effect of sediment addition overwhelmed any potential much smaller nutrient addition effects, supporting past experiments that suggest estuarine *Zostera muelleri* is relatively insensitive to nutrient concentrations (Morris et al. 2007). However, I did document interactive effect between sedimentation and season, with a stronger negative effect of sediment on seagrass in the warmer experimental month. It is well-established how temperature affects physiological functions of seagrasses such as growth, leaf elongation, photosynthesis, nutrient uptake and respiration (Bulthuis 1987). For example, the congenerics *Z. muelleri* (Kirkman et al. 1982, Larkum et al. 1984, McKenzie 1994, Ramage and Schiel 1999, Turner and Schwarz 2006), *Z. noltii* (Pérez-Lloréns and Niell 1993, Vermaat and Sand-Jensen 1987) and *Z. marina* (Jacobs 1979, McRoy 1970, Moore et al. 2014, Nienhuis 1980, Sand-Jensen 1975) generally have

higher growth, biomass and leaf area in summer than winter. It is likely that the strong inhibition from burial observed in July occurred because *Z. muelleri* had higher growth in this month and therefore also the potential for more severe inhibition of growth (see references listed above).

There are several possible reasons why I did not find any effects of fertilization. For example, the applied fertilization levels were relatively low, tidal currents may dissolve the fertilizers and urban estuarine sediments and systems may already be long-term adapted to high ambient nutrient levels. Other fertilization experiments from less eutrophic estuaries have reported increases in *Zostera* leaf density, length and biomass when exposed to somewhat higher fertilization levels than in my study (Morris et al. 2007, Orth 1977). Additionally, other studies have shown that temperature can affect both the dissolution rate of applied fertilizers (Morris et al. 2007) and the response of seagrass (*Z. marina*) to nutrient enrichment (Kaldy 2014). In contrast to fertilization, sediment addition dramatically inhibited seagrass biomass even at the lowest applied level (1 cm burial). These results are consistent with results from burial experiments with the two congeneric species, *Z. noltii* and *Z. marina*, which experience 70-90% mortality under 2-4 cm sediment burial (Cabaço and Santos 2007, Mills and Fonseca 2003). Studies on some seagrass species have, however, shown less negative or even positive effects when buried under low sediment levels such as observed for *Cymodocea nodosa*, *Posidonia oceanica* and, again, the congeneric species *Z. marina* (Duarte 1995, Manzanera et al. 1998, Mills and Fonseca 2003). As noted by Cabaço and Santos (2007), the different responses may in part be attributed to the size of the seagrass, where smaller species are less likely to survive burial, a 'size-stress-resistance' relationship also shown for seaweed-seagrass interactions (Thomsen et al. 2012b). This size-effect may be particularly relevant for *Z. noltii* and *Z. muelleri*, as they are smaller than *Z. marina*.

In addition, *Ulva* also reduced the shoot density, as shown in other drift seaweed-seagrass studies (Brun et al. 2003a, Brun et al. 2003b, Hauxwell et al. 2001, Holmer et al. 2011, Thomsen et al. 2012b). The magnitude of *Ulva* effects is likely to be context-dependent, because effects of drift seaweeds can increase with increasing temperature and seaweed abundance but decrease with seagrass size (Thomsen et al. 2012b). The negative effect from *Ulva* was likely caused by light reduction under the seaweed, limiting growth (Alcoverro et al. 1999, Brun et al. 2003a, Longstaff and Dennison 1999, Peralta et al. 2002) and shoot densities (Hauxwell et al. 2001, Longstaff and Dennison 1999). Another possible inhibition mechanism is that *Ulva* decreases sediment oxygen levels, although this explanation was not supported by the silver stick data, which suggested well-oxygenated sediments irrespective of treatments.

Finally, I did not quantify recovery potential of *Z. muelleri*. It is possible that *Z. muelleri* can recover from sediment stress through encroachment from adjacent clonal plants, by growing up through the sediment or, if sediment stress is released, through erosion, as shown for *Z. noltii* and *Halophila ovalis* (Cabaço et al. 2008), *Halodule uninervis* (Duarte et al. 1997) and *Cymodocea nodosa* (Marbà and Duarte 1995).

5.5.2 Effects on invertebrates

Effects of sedimentation on invertebrates varied with fertilization levels (with stronger negative effects under high fertilizer levels), season and presence of primary and secondary habitat formers (Hinchey et al. 2006, Nichols et al. 1978). Nevertheless, these interaction effects explained much less of the data variability compared to the effect of sediment alone (Table 1, Crain et al. 2008). Survival, growth and stress-escape mechanisms of invertebrates when exposed to sediment stress depend on species-specific adaptations. For example, bivalves are well-adapted to burial because of their muscular foot, amphipods can burrow through sediments with their exoskeleton and migrate relatively quickly with their developed legs (Hinchey et al. 2006), and many deposit feeding gastropods can move relatively fast under sediments (Bolam 2011). Indeed, the majority of estuarine taxa are typically resistant to sediment burial up to ca 10 cm depth (2 to 5 times higher sediment loading than applied in this study) and it is possible that burial depth per se is less important than sediment traits such as sediment grain size or organic matter (Nichols et al. 1978).

Invertebrates were also strongly affected by the biogenic habitat formers *Zostera* and *Ulva*, where the molluscs *Micrelenchus tenebrosus*, *Diloma subrostrata* and *Austrovenus stutchburyi* showed greatest effects. As in other studies from New Zealand, *Micrelenchus* was most abundant on seaweed (alone or in combination with *Zostera*) (Murphy 2006), *Diloma* on *Zostera* and *Zostera-Ulva* habitats (Hayward et al. 2001), and *Austrovenus* in mud and *Zostera* habitats (Hayward et al. 1999, Hayward et al. 2001, Morley et al. 1997, Murphy 2006). There were also strong seasonal effects, with more invertebrates found in November than in July. It has previously been shown that seasonal changes in *Z. marina* density (Guidetti et al. 2002, Laugier et al. 1999, Lee et al. 2006, Meling-López and Ibarra-Obando 1999) affect invertebrates, as many invertebrates can respond rapidly to changes in habitat availability, habitat complexity (Boström and Bonsdorff 2000, Frost et al. 1999, Webster et al. 1998) and food availability (Edgar and Robertson 1992, Nakaoka et al. 2001, Saunders et al. 2003, Toyohara et al. 1999). For example, Rueda and Salas (2008) showed a peak in the abundance of epifauna in summer compared to winter in *Z. marina* habitats, underpinned by changes in

seagrass leaf area. Above interpretation was supported by positive relationships between the biomass of *Zostera* (without sediment stress) and the abundance and richness of invertebrates, as previously documented for *Z. muelleri* (Battley et al. 2011) and *Z. marina* (Attrill et al. 2000, Heck Jr and Wetstone 1977, Mattila et al. 1999). These correlations, again, highlight that seagrasses increase habitat complexity, buffer environmental stressors (such as desiccation) and provide food for grazers. However, in contrast to other studies with *Ulva* (Thomsen et al. 2016a) and other seaweeds (Drouin et al. 2011, Gore et al. 1981), there was no correlation here between *Ulva* biomass and invertebrate data, possibly because very high biomass of *Ulva* can smoother some invertebrate species (Cardoso et al. 2004, Cummins et al. 2004).

More invertebrates were found (particular in the July experiment), when *Zostera* and *Ulva* co-occurred, compared to monocoltures of seagrass, thereby documenting a habitat cascade (Thomsen et al. 2010). Similar habitat cascades have been found in seagrass beds around the world, including Australia (Edgar and Robertson 1992), Denmark (Thomsen et al. 2010), Portugal (Cardoso et al. 2004), Venezuela (Stoner and Lewis 1985), and Canada (Schneider and Mann 1991b), suggesting that this type of habitat cascade is a common process. Positive effects of seaweeds were strongest on gastropods and juvenile crustaceans (Siciliano unpubl. data), where gastropods probably benefit from the high palatability and the shelter provision of *Ulva* (Mowles et al. 2011, Raffaelli et al. 1998b, Underwood 1980) whereas juvenile crustaceans may benefit more from reduced predation within the *Ulva* mats (Wilson et al. 1990b). Importantly, under sediment stress, the effects of *Ulva* (within the seagrass bed) switched from positive or neutral to negative. Under these conditions, gastropods, that were facilitated by *Ulva* in the unstressed samples, were now greatly reduced in the seagrass samples, probably because their movement were impaired and their grazing activity reduced (Airoldi and Hawkins 2007). By contrast, other more sediment-tolerant species, including several polychaetes and bivalves, were less affected. Habitat cascades are hierarchically organized processes between at least two co-occuring habitat-forming species. Habitat cascades may therefore be extra susceptible to stress because they require that both the primary and the secondary habitat formers remain healthy (Thomsen et al. 2010). In addition to sediment stress, other threats that could disrupt seaweed-seagrass habitat cascades include invasive species (Williams 2007), climate changes (Short and Neckles 1999), and eutrophication that can stimulate algal growth (McGlathery 2001) with negative effect on the seagrass (Holmer and Nielsen 2007, Thomsen et al. 2010). Clearly, more studies should integrate these types of anthropogenic stressors in experimental designs to increase our ability to predict how these ecological processes will function in the future.

5.5.3 Conclusions

In conclusion, this study demonstrated negative effects of sediments on *Z. muelleri* and its associated fauna, and that sediment stress changed the effects of seaweeds on invertebrates in the seagrass beds, from positive or neutral to negative. A key implication is that if sedimentation increases, for example if sediment-binding salt marshes, mangroves or river bank vegetation degrade, seagrass and their associated biodiversity could be severely impacted.

Tables

Table 5.1 Overview of PERMANOVA reporting the results of the factorial analysis. All factors were treated as fixed. Values represent the contribution of each test factor to the total variability of the PERMANOVA models ($\eta^2 = SS_{Explained}/SS_{Total}$). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. See Appendix 3-5.1 and 3-5.2 for complete PERMANOVA tables. Significant values are in bold (*: p = 0.05-0.01, **: p = 0.01-0.001, ***: p < 0.001). NO TEST refer to habitat conditions with only mud or *Ulva* (primary habitat former) and are therefore irrelevant for the *Zostera* responses. Note that *Ulva* in experiment 2 can be considered to be both a primary and secondary habitat former, depending on whether it was collected from the mudflat or from the seagrass bed.

Factors	Silver stick	*Zostera* leaves	*Zostera* shoot density	Abundance	Richness	Community structure
Experiment 1: interactive effects of eutrophication and sedimentation						
Fertilization (Fer)	6.70%	2.28%	0.80%	0.04%	2.45%	4.91%
Sedimentation (Sed)	3.43%	**86.88%*** **	**89.27%*** **	**47.53%*** **	**38.68%*** **	**14.19%** **
Fer × Sed	7.68%	1.82%	0.94%	10.23%	**32.89%*** **	16.42%
Experiment 2: effects of sedimentation on the habitat cascade						
2nd Habitat former (2HF)	0.23%	1.22%	**1.60%***	0.73%	0.01%	**4.82%*** **
1st Habitat former (1HF)	0.24%	NO TEST	NO TEST	0.16%	0.19%	**4.52%*** **
Sedimentation (Sed)	3.71%	**51.19%*** **	**65.11%*** **	**36.02%*** **	**39.23%*** **	**13.24%*** **
Elevation (Ele)	2.09%	0.47%	0.08%	0.57%	0.00%	1.48%
Season (Sea)	0.20%	**11.35%*** **	0.35%	**2.75%** **	1.41%	**4.72%*** **
2HF × 1HF	1.85%	NO TEST	NO TEST	0.04%	0.25%	0.60%
2HF × Sed	2.68%	1.15%	0.70%	**1.79%***	0.04%	1.19%
2HF × Ele	1.48%	0.64%	**1.19%***	**4.48%** **	**2.73%***	0.81%
2HF × Sea	0.87%	0.16%	0.05%	1.65%	0.49%	1.23%
1HF × Sed	0.16%	NO TEST	NO TEST	**6.04%*** **	1.73%	**2.38%** **
1HF × Ele	0.02%	NO TEST	NO TEST	**6.16%*** **	**9.06%*** **	**2.31%*** **
1HF × Sea	2.05%	NO TEST	NO TEST	0.90%	**2.20%***	0.94%
Sed × Ele	0.08%	0.70%	0.35%	**3.55%** **	1.35%	**2.18%** **
Sed × Sea	1.57%	**16.16%*** **	**21.11%*** **	**2.41%***	0.01%	**2.20%** **
Ele × Sea	0.76%	0.01%	0.43%	0.37%	1.34%	**1.95%***

2HF × 1HF × Sed	0.56%	NO TEST	NO TEST	0.01%	0.43%	0.33%
2HF × 1HF × Ele	4.89%	NO TEST	NO TEST	0.00%	0.24%	0.40%
2HF × 1HF × Sea	1.36%	NO TEST	NO TEST	0.29%	0.31%	0.58%
2HF × Sed × Ele	1.36%	0.09%	0.67%	0.09%	0.46%	1.20%
2HF × Sed × Sea	0.47%	0.04%	0.28%	0.36%	1.15%	**2.07%****
2HF × Ele × Sea	0.03%	0.06%	0.03%	0.02%	0.02%	1.25%
1HF × Sed × Ele	0.71%	NO TEST	NO TEST	0.36%	0.14%	0.39%
1HF × Sed × Sea	0.01%	NO TEST	NO TEST	0.22%	0.02%	0.22%
1HF × Ele × Sea	0.05%	NO TEST	NO TEST	0.28%	1.92%	1.19%
Sed × Ele × Sea	1.50%	1.02%	0.06%	0.00%	0.00%	0.89%
2HF × 1HF × Sed × Ele	2.12%	NO TEST	NO TEST	**1.81%***	0.13%	0.45%
2HF × 1HF × Sed × Sea	0.00%	NO TEST	NO TEST	0.00%	1.78%	0.55%
2HF × 1HF × Ele × Sea	1.34%	NO TEST	NO TEST	0.01%	0.38%	0.30%
2HF × Sed × Ele × Sea	0.06%	0.27%	0.26%	0.11%	0.36%	0.77%
1HF × Sed × Ele × Sea	0.00%	0.00%	0.00%	0.00%	0.25%	**1.78%***
2HF × 1HF × Sed × Ele × Sea	0.00%	NO TEST	NO TEST	0.11%	0.00%	**1.51%***

Figures

Figure 5.1 Experiment 1, testing for the effects of sedimentation and fertilization on blackened length of silver sticks (A), *Zostera muelleri* leaf biomass (B), shoot density (C), invertebrate abundance (D) and richness (E) for four levels of sediments (S_0, S_1, S_2 and S_4 = adding 0, 1, 2 and 4 cm sediments) and fertilizers (F_0, F_2, F_4, F_8 = adding 0, 2, 4, and 8 fertilizer sticks). Sample core = 0.0064 m^2. Error bars = 1 SE, n = 3. Different letters indicate significant differences as detected by pair-wise t-test comparisons.

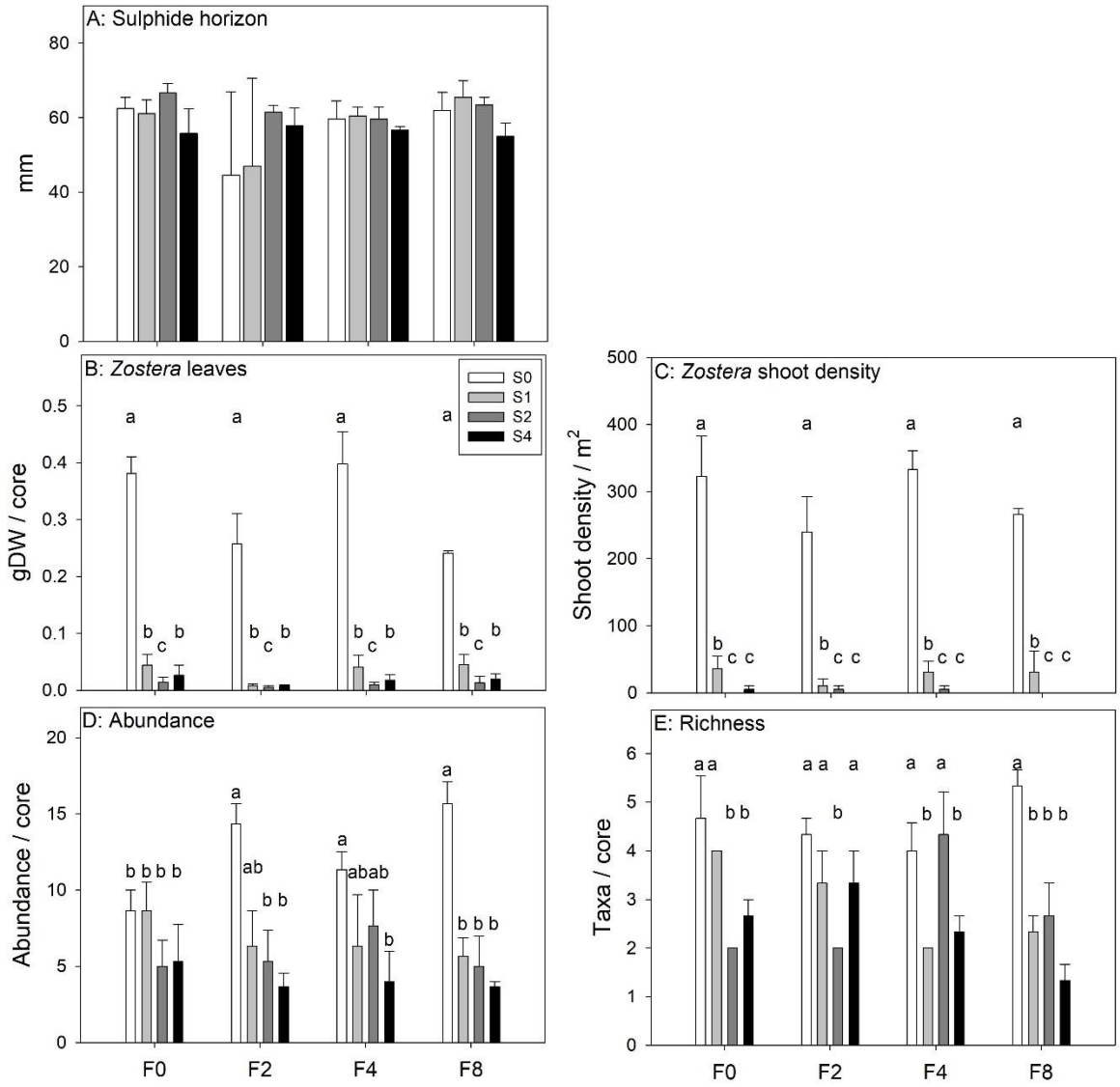


Figure 5.2 Experiment 1, testing for the effects of sedimentation and fertilizers on invertebrate community structure. MDS plot was based on Bray-Curtis similarity for four levels of sediments (different grey scales: S_0, S_1, S_2 and S_4 = adding 0, 1, 2 and 4 cm) and fertilizers (different symbols: F_0, F_2, F_4, F_8 = adding 0, 2, 4, and 8 fertilizer sticks). Data were square-root transformed prior to analysis. n = 3. A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: small juvenile crabs, 2: *Austrovenus stutchburyi*). Stress: 0.26.

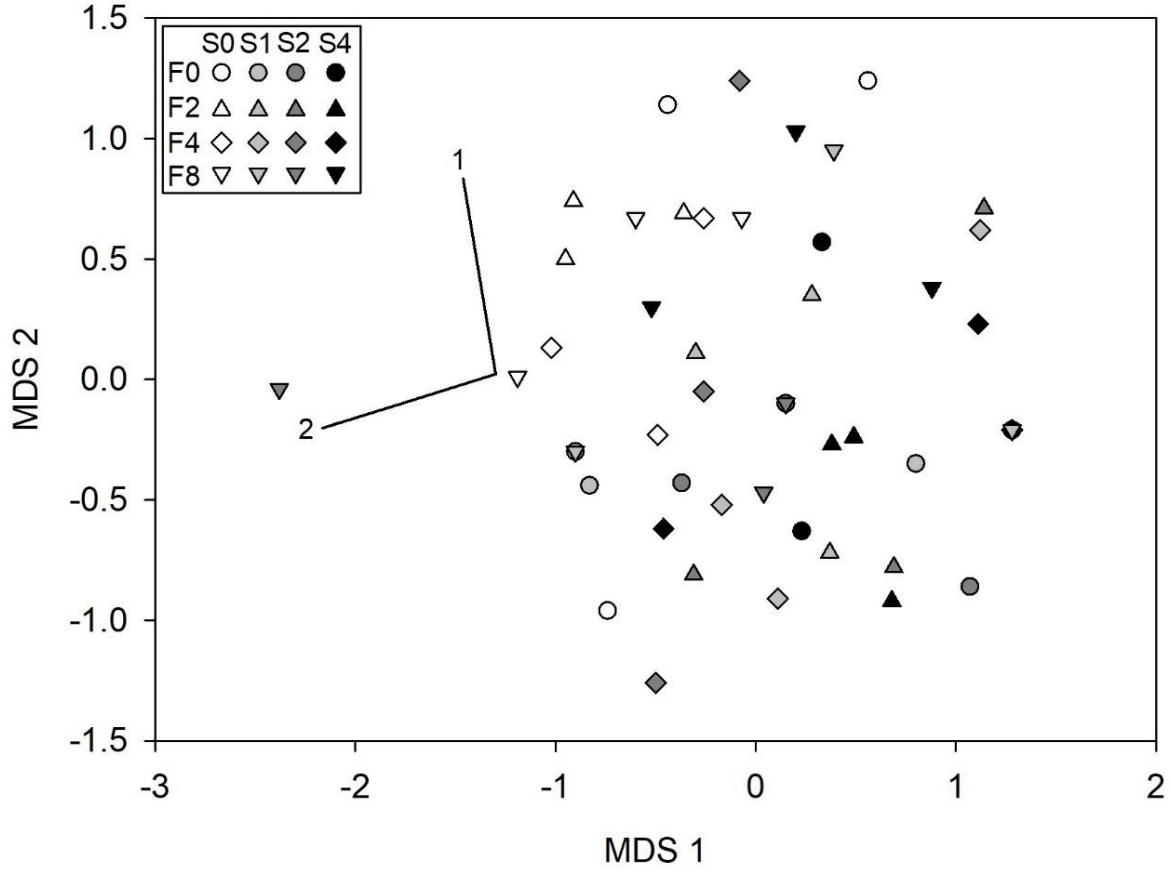


Figure 5.3 Experiment 2, testing for effects of adding sediments (+) and drift *Ulva* sp. (U) to muddy (M) and *Zostera muelleri* (Z) habitats, on blackened length of silver sticks (A-B), *Zostera* leaf biomass (C-D) and shoot density (E-F) and invertebrate abundance (G, H) and richness (I, J) in both summer (left) and winter (right) seasons. Sample core = 0.0064 m^2. Error bars = 1 SE, n = 6. The test factors 'Elevation' was pooled. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refer to the 'sedimentation' test factor, lower case letters to the '1st habitat former × 2nd habitat former' interaction.

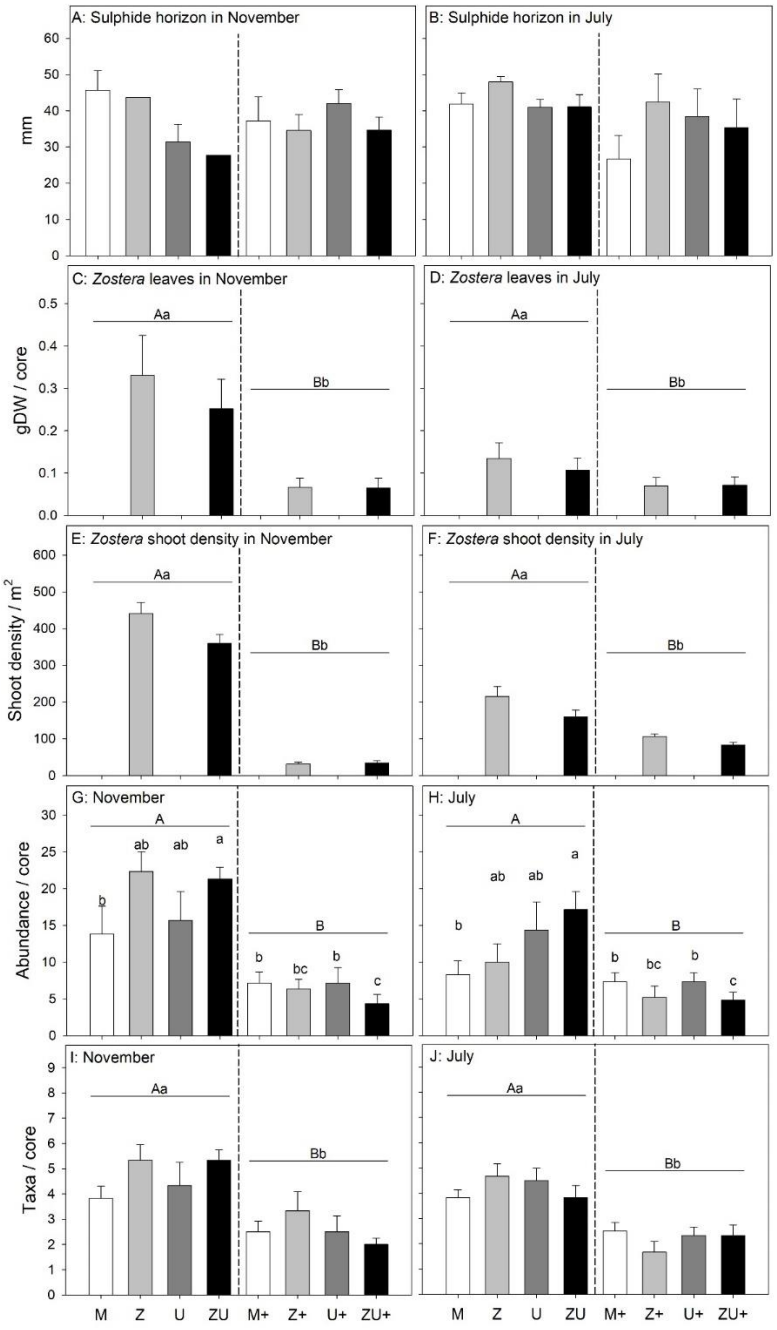


Figure 5.4 Experiment 2, testing for effects of adding sediments (+) and drift *Ulva* sp. (U) to muddy (M) and *Zostera muelleri* (Z) habitats, on invertebrate multivariate community structure. MDS plot was based on Bray-Curtis similarity. For simplicity, data were split into July and November experiments but results are from the same analysis and the two plots can be superimposed on each other (and therefore have the same taxa vectors). Data were square-root transformed prior to analysis. The test factor 'Elevation' was pooled. n = 6. A SIMPER analysis was used to determine which species contributed up to 50% of the data variability (1: *Micrelenchus tenebrosus*, 2: *Diloma subrostrata*, 3: *Austrovenus stutchburyi*, 4: errant polychaetes, 5: *Macomona liliana*, 6: *Cominella glandiformis*). Stress: 0.26. One outlier sample was removed from the B plot: Z+ (-9.75, 0.00).

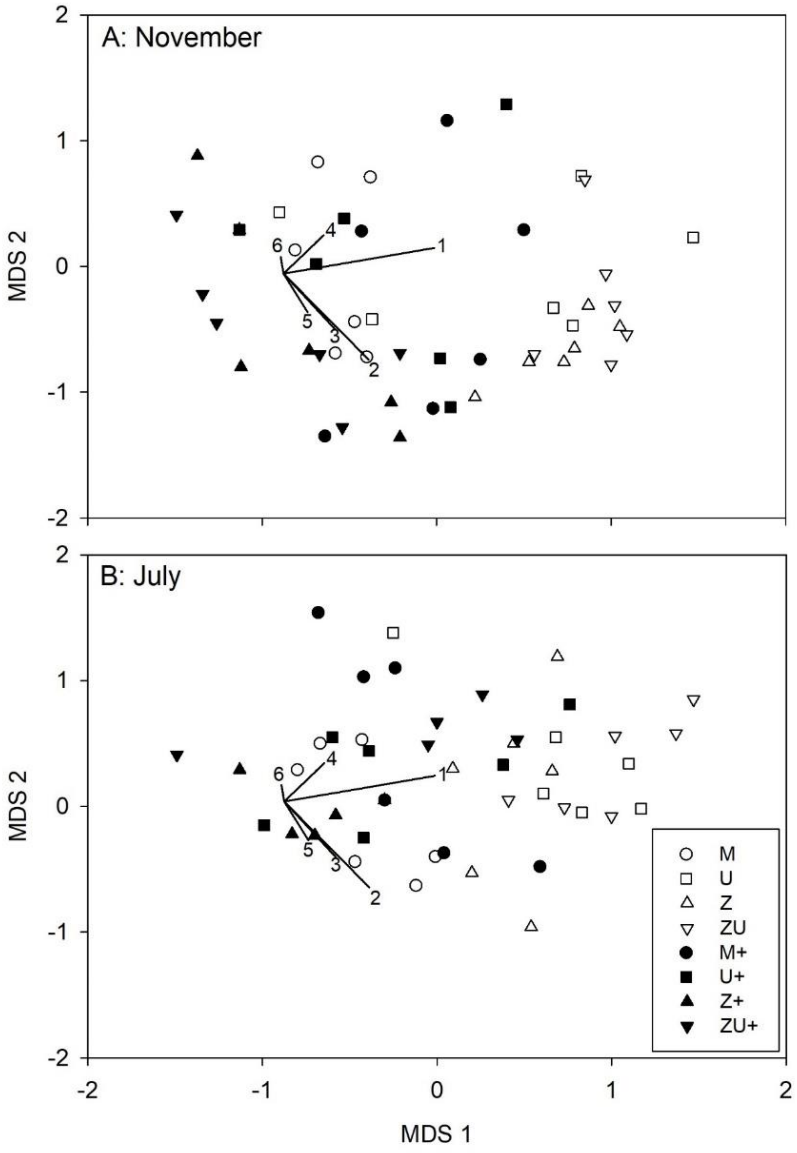
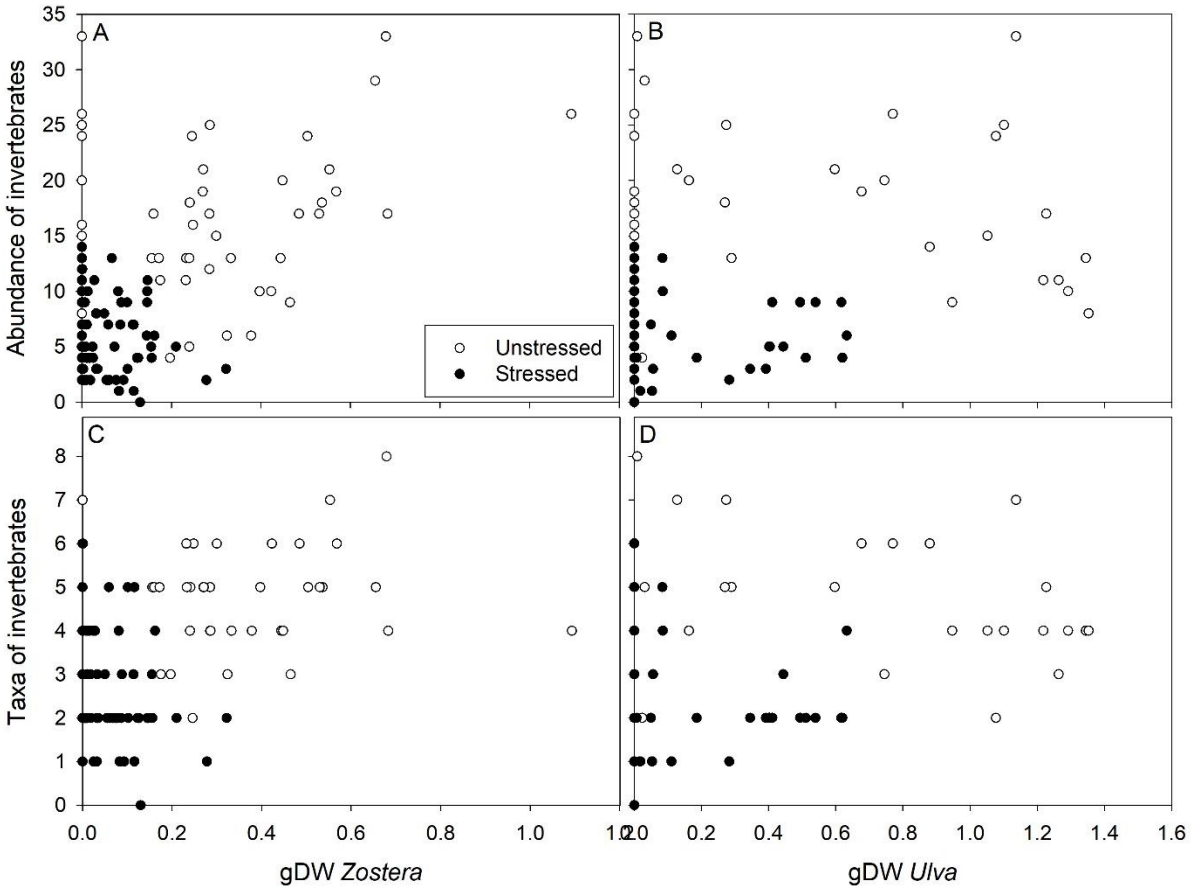


Figure 5.5 Correlation between the biomass of *Zostera muelleri* (A, C) and the seaweed *Ulva* sp. (B, D) vs abundance (A, B) and taxonomic richness (C, D) of invertebrates. Experiment 1: n = 48, Experiment 2: n = 96. Black and white points are samples with and without sediment addition stress, respectively, whereas circles and squares represent samples from experiment 1 and experiment 2, respectively. Spearman's rank correlation analyses were carried out separately for unstressed and stressed samples. Stressed: A: $r_{Spearman} = -0.18$, $p = 0.1$, B: $r_{Spearman} = -0.10$, $p = 0.38$, C: $r_{Spearman} = -0.03$, $p = 0.76$, D: $r_{Spearman} = -0.15$, $p = 0.17$. Unstressed samples: A: $r_{Spearman} = 0.36$, $p = 0.005$, B: $r_{Spearman} = 0.28$, $p = 0.03$, C: $r_{Spearman} = 0.25$, $p = 0.054$, D: $r_{Spearman} = 0.01$, $p = 0.97$.



CHAPTER 6: Are habitat cascades similar among morphologically comparable canopy-forming hosts and epiphytes?

6.1 ABSTRACT

It is well established that primary habitat-forming species characterized by widely different morphologies affect secondary habitat-forming epiphytes and epifaunal communities differently, both directly and indirectly through habitat cascades. However, no studies have tested the opposite hypothesis, that is, if morphologically similar congeneric primary habitat formers support similar epiphytes with similar direct and indirect cascading effects on invertebrate communities. This hypothesis was tested with mensurative and manipulative experiments using three co-existing morphologically similar congeneric marine macroalgal hosts from the South Island of New Zealand: the canopy-forming fucoids *Cystophora torulosa*, *C. scalaris*, and *C. retroflexa*. Diverse communities of small mobile gastropods (250-1000 µm) associated with the three host species were sampled with and without attached epiphytes from tide pools at 2 reefs (> 1 km apart) from 4 sites across a latitudinal gradient (> 100 km apart). In two follow-up field experiments, defaunated primary habitat formers (including the morphologically different fucoid *Hormosira banksii*), epiphytes (*Polysiphonia decipiens* and *Jania micrarthrodia*) and artificial epiphyte mimics were out-transplanted to tide pools to quantify colonizing gastropod communities. Results from the survey and the first field experiment led me to reject the initial hypothesis, because the three congeneric hosts supported different gastropod communities and had different cascading effects. I also found positive effects of epiphytes on the abundances and richness of gastropods. The second experiment documented that epiphytic biomass had a significant positive effect on gastropod abundances for both *C. scalaris* and *H. banksii*, and that artificial mimics and live epiphytes were colonized by similar gastropod communities, suggesting that structural effects are more important than whether the habitat is 'edible'. Finally, an analysis of morphological traits of the primary and secondary habitat formers suggested that traits, like biomass, surface-area and fractal dimension are good predictors of the strength of habitat cascades. These results highlight that rocky shore habitat cascades, at least on small scales, can increase biodiversity, and that even superficially similar primary and secondary habitat formers can support different communities of mobile gastropods. These findings caution against classic analyses of form-functional grouping that pool similar-looking species, thereby overlooking subtle direct and indirect effects associated with biogenic habitat formation.

6.2 INTRODUCTION

Indirect facilitations represent ecological interactions whereby a primary species facilitates a focal species in the presence of a secondary species (Thomsen et al. 2010). These types of ecological processes have long been studied but were first named in 1980 (Davidson 1980). A specific type of indirect facilitation occurs through sequential positive species-interactions ('facilitation cascades', *sensu* Thomsen et al 2010). Facilitation cascades have been documented from a variety of ecosystems (Altieri et al. 2007, Angelini et al. 2011, Bell et al. 2014, Bishop et al. 2012, Bishop et al. 2013, Bishop et al. 2009, Thomsen et al. 2016b, Thomsen et al. 2010) but remain understudied compared to indirect facilitation processes occurring through enemy interactions, like trophic cascades or keystone predation (Paine 1966, 1980, Thomsen et al. 2016b).

Among the different type of facilitation cascades, the most commonly documented types are the 'habitat cascades' that occur through sequential biogenic habitat formation and modification (Bruno and Bertness 2001, Ohgushi 2005, Thomsen et al. 2010). For example, Hughes (2014) demonstrated that primary habitat-forming mangrove pneumatophores (*Avicennia marina*, primary habitat former) provide attachment space (i.e., habitat) to intermediate habitat-forming oysters (*Saccostrea glomerata*, secondary habitat former) with a net positive effect on the abundance and richness of the invertebrate communities. Habitat cascades are common in many different systems (Thomsen et al. 2018, Thomsen et al. 2010), but particularly in ecosystems where epibiosis is a prevailing process. For example, it is well documented that epiphytes can increase biodiversity of invertebrates in forests (Cruz-Angòn et al. 2009, Díaz et al. 2012, Ellwood and Foster 2004, Nadkarni and Longino 1990, Yanoviak et al. 2007, Zotz and Bader 2011), seagrass beds (Bologna and Heck 1999, Edgar and Robertson 1992, Lewis III and Stoner 1983, Stoner and Lewis 1985) and rocky shores (Buzá-Jacobucci and Pereira-Leite 2014, Pavia et al. 1999, Thomsen et al. 2016b).

Predictors of habitat cascades. The above studies have largely tested if secondary habitat formers increase biodiversity based on simple 'presence-absence' designs (i.e., with or without the presence of a secondary habitat former, but see Bishop et al., 2009 and Bologna and Heck, 1999 for more specific tests of mechanisms). However, mechanistic models and experiments are needed to improve predictions about the strength of habitat cascades. It has been suggested that the strength of habitat cascades depends on the amount of secondary habitat formers (providing more habitat space) (Bishop et al. 2012, Bishop et al. 2013, Gribben et al. 2013) and

form-functional trait differences between the primary and secondary habitat former (Irving and Bertness 2009, Bishop et al. 2013, Gribben et al. 2013), as different species provide different niches for different focal species (Angelini and Silliman 2014, Thomsen et al. 2010). Taxonomically closely related species typically show similar form-functional traits compared to taxonomically distant species (Webb et al. 2002). Artificial mimics of biogenic habitat formers have, in the past, been an important tool to test how form-functional traits modify habitat use, because mimics have no shared co-evolutionary histories, cannot be consumed, but can be easily manipulated and replicated. For example, Hall and Bell (1988) used mimics of seagrass blades (primary habitat former) and its algal epiphytes (secondary habitat former) to document a habitat cascade in a seagrass bed, and Martin-Smith (1993) used macroalgal mimics to document that *Sargassum* mimics (primary habitat former) provided substrate for naturally colonizing epiphytes (secondary habitat former), which then supported more invertebrates, compared to *Sargassum* mimics without epiphytes.

Comparing habitat cascades for single vs multiple habitat-forming species. Most studies of habitat cascades compared effects associated with a single species of both the primary and secondary habitat formers, for example describing effects on focal species associated with the epiphytic macroalga *Notheia anomala* attached to *Hormosira banksii* (Thomsen et al. 2016b), *H. banksii* entangled around pneumatophores of the mangrove *A. marina* (Bishop et al. 2013, Bishop et al. 2009), ribbed mussel embedded in marshes of the cordgrass *Spartina alterniflora* (Altieri et al. 2007, Altieri et al. 2010), the green seaweed *Ulva* attached to the cockle *Austrovenus stutchburyi* (Thomsen et al. 2016a), or the red alga *Gracilaria comosa* entangled around the leaves of the seagrass *Halophila ovalis* (Thomsen et al. 2012a). However, to truly replicate and test if different form-functional traits affect habitat cascades it is necessary to include more than one primary and/or secondary habitat former. Few studies have compared such habitat cascades based on multiple primary and secondary habitat formers: Dijkstra et al. (2012) showed that co-occurring *S. alterniflora* (primary habitat former) and two secondary fucoid seaweeds (*Ascophyllum nodosum* and *Fucus vesiculosus*) facilitated marsh snails; Thomsen et al. (2013) tested for the effect of the invasive seaweed *Gracilaria vermiculophylla* (secondary habitat former) co-occurring with two native primary habitat formers (the seagrass *Zostera marina* and *Mytilus edulis*) on mobile invertebrates; similarly, Hughes et al. (2014) investigated the individual roles of two secondary habitat formers, the seaweed *H. banksii* and the oyster *Saccostrea glomerata*, entangled around and attached to mangrove pneumatophores (primary habitat former), respectively, finding positive effects of the secondary habitat former

on mobile invertebrates; finally, Mendez et al. (2015) tested the effects of the invasive barnacle *Balanus glandula* (secondary habitat former) attached to either natives *S. alterniflora* or native mussels (i.e., two different primary habitat formers). However, these studies all compared taxonomically and form-functionally different primary or secondary habitat formers (bivalve vs seagrass, plant vs mussel, seaweed vs bivalve) making it relatively straightforward to interpret positive effects on species diversity where secondary habitat formers add new niches. However, to my knowledge, no studies have compared habitat cascades among congeneric habitat formers with similar evolutionary and ecological traits or among multiple primary and secondary habitat formers simultaneously.

Rocky intertidal habitats are characterized by strong physical stress gradients (Longtin et al. 2009, Menge and Branch 2001, Stephenson and Stephenson 1949). In these systems, canopy-forming seaweeds provide habitat for invertebrates and buffer stressors related to desiccation, temperature and wave action (Davison and Pearson 1996, Garbary 2007). In addition, substrate space is often a limiting resource for sessile species (Dayton 1971). Many species have, however, adapted to limited space by attaching to and growing on other sessile species (Hay 1986, Seed and O'Connor 1981, Wikström and Kautsky 2004). The presence of these epiphytic species can affect epifaunal communities, for example, by providing shelter and/or food (Jones and Thornber 2010, Martin-Smith 1993, Viejo 1999, Wikström and Kautsky 2004), additional settlement space (Karez et al. 2000, Pavia et al. 1999, Viejo and Åberg 2003) or increasing structural complexity (Martin-Smith 1993).

Here I studied seaweed habitat cascades from rocky intertidal systems in the South Island of New Zealand. These shores are dominated by co-occurring canopy-forming fucoid seaweeds such as *Cystophora torulosa*, *C. scalaris*, *C. retroflexa* and *Hormosira banksii* (Schiel and Lilley 2007, 2011, Tait and Schiel 2011, Womersley 1964, Womersley 1987). The three *Cystophora* species have very similar morphology, with a single flexible axis with branched laterals and terminal receptacles and conceptacles (Adams 1997, Womersley 1964) compared to *H. banksii*, with multiple flexible axes made up of strings of pneumatocysts originating from the holdfast. The role of these canopy-forming species as substrate for epiphytes is well described (Ducker et al. 1976, Hallam et al. 1980, Schiel 2006, Thomsen et al. 2016b).

In addtion to providing attachment space for epiphytes, *Cystophora* spp. and *H. banksii* also provide habitat to diverse and ubiquitous gastropod communities. These slow-moving shell-forming taxa are a significant part of marine invertebrate communities associated with seaweeds (Siciliano unpubl. data, Cowles et al. 2009, Taylor 1998a, b, Thomsen et al. 2016b).

Furthermore, gastropods are easy to sample (Smith 2005), robust to handle, can be identified to 'morpho-species' (Chapman and Underwood 2008, Smith 2005) and represent a heterogeneous group with different ecological functions (Chapman and Underwood 2008). Gastropods are therefore great model organisms and representative of wider intertidal invertebrate communities (Chapman and Underwood 2008, Smith 2005) that can be used to predict ecological patterns across spatio-temporal scales (Smith 2005).

Five hypotheses were tested in relation to *Cystophora* habitat cascades: (i) the three taxonomically related and morphologically similar primary habitat formers (*Cystophora* spp.) are inhabited by similar gastropod communities; (ii) epiphytes on *Cystophora* increase biodiversity of gastropods; (iii) these patterns are consistent across latitudes, reefs and seasons; (iv) more gastropods are found on live and abundant epiphytes than non-living mimics and sparse epiphytes; (v) the gastropod communities associated with *Cystophora* are different from communities associated with the morphologically and taxonomically different *H. banksii*. The first three hypotheses were addressed with a survey and a field experiment, whereas last two hypotheses were tested in a second field experiment and a laboratory experiment.

6.3 MATERIALS AND METHODS

6.3.1 Study region

This study took place in the rocky intertidal zone on the east coast of the South Island of New Zealand. Field surveys were conducted on reefs at Cape Campbell (41°43'36.685"S, 174°16'31.962"E), Kaikoura (42°24'51.707"S, 173°42'18.472"E), Pile Bay in Lyttelton Harbour (43°37'16.126"S, 172°45'42.736"E) and Moeraki (45°21'31.907"S, 170°51'43.823"E). The four latitudes span a 4° latitudinal gradient, covering > 550 km coastline and have a temperature gradient of ca 3°C (mean annual SST = 11°C at Moeraki vs 14°C at Cape Campbell (Schiel 2011). However, other factors may co-vary with this temperature gradients such as day-length, water turbidity, wave exposure, grazing and predation pressures. The reefs from Cape Campbell, Kaikoura and Moeraki extend approximately 150 m from the upper intertidal to the subtidal zones and are generally protected from severe wave action by off-shore reefs and have a coastal topography that deflects swells (Ramage and Schiel 1999). In Pile Bay the reef only extends ca 50 m and is located in the outer part of a protected large bay (i.e., are still exposed to oceanic swells). The three northern reefs are part of the East Coast South Island biogeographic coastal zone whereas Moeraki is within the Southern South Island zone (Schiel 2011). All reefs are exposed to the Southland Current

and the intertidal platforms are dominated by the same canopy-forming seaweeds, in particular *C. torulosa*, *C. scalaris*, *C. retroflexa* and *H. banksii* (Schiel 2011). All sampling was carried out during low tide in sheltered middle and low shore intertidal tide pools and channels (i.e., samples were submerged at the time of collection).

6.3.2 Spatial survey: effects of primary and secondary habitat formers across latitudes

Fronds were collected from the three primary habitat-forming *Cystophora* species (*C. retroflexa*, *C. scalaris*, and *C. torulosa*) between November 2014 and February 2015. All three species were collected with and without attached secondary habitat-forming epiphytes. Collections were made at two reefs (> 500 m apart) for each of the 4 latitudes (> 100 km apart). At each reef, samples from the three *Cystophora* species were collected from four pools or channels. Ca 15 cm of fronds were cut off of each *Cystophora* species, with and without epiphytes, and quickly transferred to a sealed plastic bag to minimize loss of mobile gastropods. Bags were stored in chilly bins before being transported to the lab for processing. The sampling design was: 3 *Cystophora* species (primary habitat former) × 2 epiphyte levels (± epiphyte, secondary habitat former) × 4 latitudes × 2 reefs × 4 tide-pools/channels per reef (replicates). I found four replicated pools/channels with the three *Cystophora* species without epiphytes and statistical tests about primary habitat former effects without epiphytes are therefore fully balanced. However, there were several tide-pools and reefs where I could not find some of the *Cystophora* species with epiphytes (Appendix 3-6.1). Furthermore, epiphytic species identity varied between reefs. My primary objective was collecting *Cystophora* species with epiphytic *Jania micrarthrodia* and *Polysiphonia decipiens* (hereafter *Jania* and *Polysiphonia*) because these epiphytes are common on most of the sampled reefs and are generally common along the east coast of New Zealand (Adams 1997). Furthermore, these two species represent different life-histories such as calcified and non-calcified fronds, and are relatively easy to remove and add manually to the different *Cystophora* species. Nevertheless, these epiphytes were absent from a few reefs and I therefore also collected host fronds with different epiphytic species (Appendix 3-6.1).

6.3.3 Field experiments

Two field experiments were conducted on the Kaikoura peninsula to test if gastropod communities varied among primary habitat formers, epiphyte species and seasons. For each experiment, ca 15 cm distal fronds of each *Cystophora* species without epiphytes were collected from tide-pools. All fronds were transported to the laboratory where they were de-

faunated by shaken and rinsing with seawater. Preliminary trials had shown that this method removed > 95% of all mobile invertebrates (Siciliano, unpubl. data). Epiphytes were collected from the same sites and defaunated before being added to the distal segment of the host species with cotton twine. *Cystophora* species were attached to 1-m long heavy chains with cable ties (all fronds where separated from each other by ca 50 cm). A pendant Hobo light and temperature logger was attached to each chain, recording temperature and light intensity during each experiment at 20 minute intervals. Finally, chains were haphazardly placed in ca 50 cm deep pools or channels. The experiments ran for 2 weeks, after which samples were collected by cutting the cable tie and swiftly adding the seaweed to a sealed plastic bags before being transported to the laboratory in chilly bins.

6.3.4 Experiment 1: effects of primary and secondary habitat formers across seasons

The first experiment tested if secondary production differed between gastropods inhabiting the three *Cystophora* species with and without two different epiphyte species (*Jania* and *Polysiphonia*). This experiment was carried out at Wairepo reef, in Kaikoura, and emulated the survey but controlled the abundance of the seaweed and the initial gastropod community (as it was removed). The experimental design was as follow: 3 *Cystophora* species × 3 epiphyte spp. (0, *Jania*, *Polysiphonia*) × 2 seasons (winter and summer) × 4 replicates. The winter and summer experiment were set up 1st June and 13th December 2015, respectively.

6.3.5 Experiment 2: effects of secondary habitat former biomass and type across seasons

The second experiment was composed of two sub-experiments. The first sub-experiment (2a) tested if gastropod communities changed with epiphyte biomass and if the epiphyte was 'alive' (compared to a non-living epiphyte mimic) using five combinations of epiphyte biomasses and epiphyte types in the following experimental design: 5 epiphytes levels/types (control, living vs mimic, low vs high biomass) × 2 reefs (Wairepo and South Bay, in Kaikoura) × 2 seasons × 4 replicates. *C. scalaris* and *Polysiphonia* were chosen as primary and secondary habitat-forming species, respectively, because the survey showed that these species were inhabited by abundant gastropod communities across study reefs (Appendix 6.1). *Polysiphonia* was added to *C. scalaris* in a high and low biomass treatment (0.17 ± 0.02 vs 0.06 ± 0.02 per gDW 1st + 2nd HF), where the high level corresponded to typical high levels found in the field survey. Similar high and low biomass of a non-living *Polysiphonia* mimic were added to *C. scalaris*. These mimics were created from plastic fry-pan scrapers, that were cut, twisted and wrapped to provide a shape similar to *Polysiphonia*. Adding mimics allowed me to test if gastropods

mainly colonized live and edible habitat or if they also colonized non-living structures. The winter and summer experiments were setup on 24th September and 13th December 2015, respectively.

I also tested if *C. scalaris* with and without epiphytic *Polysiphonia* affects gastropod communities differently than the co-occurring canopy-forming *Hormosira banksii* and its obligate epiphyte *Notheia anomala* (hereafter *Notheia*). The same 5 epiphyte levels were used, that is, *Hormosira* (primary habitat former) was added to chains without epiphytes and with high and low biomass of both *Notheia* and a non-living plastic mimic (secondary habitat formers, the same mimic as used for *C. scalaris*). This sub-experiment (2b) was only carried out in summer, set up on 13th December. All seaweed collections, manipulations and field procedures were similar to experiment 1.

6.3.6 Experiment 3: effects of grazing

A laboratory experiment tested if the gastropod community grazes on the primary (*Cystophora* spp.) and secondary habitat formers (*Jania* and *Polysiphonia*). The experimental design was as follows: 11 host-epiphyte treatments (3 *Cystophora* spp. × 3 epiphytes levels + 2 controls, i.e., *Jania* and *Polysiphonia* alone) × 2 grazers levels (± ca 70 gastropods) × 2 'seasons' × 3 replicates. Ca 0.4 gWW of a each *Cystophora* species (with and without 0.3 gWW of epiphyte) were added to 50 ml vials together. In the grazing treatments natural densities of ca 70 gastropods were added. Seaweeds were blotted 3 times with paper towels and weighted before and after the experiment. Vials were covered with a 0.5 mm mesh to prevent gastropods escaping and to exchange waters. Water in the tanks was changed two times per day, to ensure oxygenation, prevent self-shading, and to simulate water flushing in tidal channels and pools. The experiment was conducted at 18°C and 13°C to match typical summer and winter temperatures, by using separate tanks equipped with aquarium heaters (2× Eheim Jager 3616 in each tanks). The experiment ran for one week. All treatments were monitored twice per day with 8-hour difference, where I estimated the percentage of the 70 gastropods that were out of the water, in the water or attached to seaweeds.

6.3.7 Morphological traits of habitat formers

Morphological traits were quantified and compared between the habitat-forming species sampled in the surveys and experiments. Traits included surface area:dry weight ratios, fractal dimension, circularity (a measure of 'roundness', ranging from 0 for an infinitely elongated polygon, to 1 for a perfect circle; Sedgewick 2010) and lacunarity (an index of 'gappiness' or

'visual texture', considered a measure of heterogeneity; Ferreira and Rasband 2012, Karperien 2007). Ten individuals of *C. retroflexa*, *C. scalaris*, *C. torulosa* and *Hormosira, Jania, Polysiphonia* and the *Polysiphonia* mimic were blotted three times with paper towels and spread out on a white background to enhance the contrast for subsequent image analysis. For each sample a picture was taken with a Canon PowerShot G7X Mark II with ruler as a scaling reference. Each frond was then dried for 48 h at 55°C or until no further weight loss could be detected and its dry weight measured on a scale with three digits. Using Photoshop, each image was converted to grey scale and thresholded to binary images. Surface area:dry weight and circularity was calculated in ImageJ (Rasband 1997-2016), as was fractal dimensions and lacunarity, using the plugin FracLac (Karperien 1999-2013).

6.3.8 Laboratory analysis

In the laboratory, samples were rinsed onto a 250 µm sieve to collect mobile gastropods. Attached epiphytes were thereafter removed, identified and weighed (gDW after drying at 55°C for 48 h or until no further weight loss could be detected). Gastropods were counted, identified to morpho-species (Appendix 3-6.2 for examples) under a dissecting microscope at 40× magnification, and preserved in 70% ethanol.

6.3.9 Statistical analysis

I tested for effects of primary and secondary habitat formers on (i) total abundance, (i) richness of morpho-species and (i) multivariate community structure. Data were standardized per gram dry weight of the total association of habitat-forming seaweeds (i.e, gDW 1^{st} or gDW $1^{st}+2^{nd}$ habitat former) and square-root transformed to reduce the statistical importance of a few dominant morpho-species and decrease variances for the most abundance taxa. I tested for effects of primary habitat former species, latitude, seasons, and epiphyte type and biomass with permutation-based factorial analysis of variance (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. In the second experiment, data from *Cystophora* species without epiphytes (‘controls’) were not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type (live vs mimic) and biomass (low vs high). All factors were treated as fixed and ‘Reef’ was nested in ‘Latitude’. Results were considered significant if $p \leq 0.05$. Data not meeting the criteria of homogeneity (Levene’s test) and normality (Shapiro-Wilk) were square root transformed. For each dataset I

used Spearmans' rank correlations to relate biomass of the primary and secondary habitat formers to both gastropod abundances and richness. Data from the grazing experiment (percentage change in wet weight) were square-root transformed and analyzed with a 1-way fixed Anova. Morphological trait data were analyzed individually with Anova and combined with PERMANOVA, to test if traits differ among different species of primary and secondary habitat formers. Morphological data were square-root transformed and normalized, and significant effect was followed up by post-hoc pair-wise t-tests (Anderson et al. 2008).

6.4 RESULTS

A total of 101,067 gastropods, representing 66 morpho-species (Appendix 3-6.3 for examples) were counted and identified in the survey and two field experiments from 361 collected fronds with a total primary and secondary habitat former biomass of 1,381 and 371 gDW, respectively. The most abundant families were Hydrobiidae, Pyramidellidae and Ellobiidae. Every single collected gastropod was < 1 cm and most were < 0.5 mm.

6.4.1 Spatial survey: effects of primary and secondary habitat formers across latitudes

Gastropod abundance. A total of 112 *Cystophora* fronds were collected in the survey. These fronds were inhabited by 34 algal epiphytic species and almost 40,000 gastropods (56 morpho-species). I found 8 examples where second order epiphytes were attached to *Cystophora* epiphytes. The most common epiphytes were *Jania micrarthrodia* (38%), followed by *Colpomenia* sp. (19%), *Lophothamnion hirtum* (17%), *Polysiphonia* sp. (12%) and *Echinothamnion* sp. and *Champia novae-zelandiae* (both 10%).

I found several complex higher order interactions. For example, I found a significant 3-factor interaction Latitude × 1st HF × 2nd HF (Table 6.1, $p < 0.05$; $\eta^2 = SS_{Explained}/SS_{Total}$; η^2 = 3.30%). This interaction indicated that gastropods were affected differently by different combinations of these three factors, but typically with highest densities when epiphytes were present (e.g., at Cape Campbell for *C. scalaris*, $p = 0.004$, E+ vs E-: 60.90 ± 8.85 ind. / gDW 1st+2nd HF vs 21.68 ± 2.63; at Kaikoura for *C. retroflexa*, $p = 0.02$, E+ vs E-: 80.46 ± 26.59 vs 37.03 ± 9.35 at Pile Bay for *C. torulosa*, $p = 0.003$, E+ vs E-: 38.83 ± 5.87 vs 11.96 ± 3.55). A significant Reef(Latitude) × 1st HF explained ca 4% of the data variability, suggesting that gastropods are differently affected by different primary habitat former identity across reefs and latitudes. Among the single test factors, Reef explained most of the data variability ($\eta^2 > 9\%$), followed by the second habitat former presence ($\eta^2 < 7\%$), Latitude ($\eta^2 > 6.5\%$) and primary

habitat former identity (η^2 > 6%). Samples from Moeraki were inhabited by fewer gastropods (27.16 ± 2.77) compared to the other locations (Cape Campbell = Kaikoura = Pile Bay: 45.36 ± 5.16, 49.61 ± 7.24, 45.43 ± 5.56). As hypothesized, more gastropods inhabited *Cystophora* with epiphytes (51.08 ± 3.97) than without (27.31 ± 2.85) (p = 0.011, Fig. 6.1A-D). I also found more gastropods associated with *C. retroflexa* (53.40 ± 5.98) than *C. scalaris* (40.50 ± 3.61) and least with *C. torulosa* (35.12 ± 5.36) (Fig. 6.1A-D).

Gastropod richness. The only significant interaction was Reef(Latitude) × 2nd HF (Table 6.1), explaining just 3% of data variability, suggesting that epiphytes have different effects at different reefs. Richness was also affected by Latitude (p = 0.001, η^2 > 20%), Reef (p = 0.001, η^2 = 9.8%) and 1st HF (p < 0.05, η^2 = 3.2%). More specifically, more taxa were found in Pile Bay and Kaikoura (4.86 ± 0.48 taxa / gDW 1st+2nd HF and 4.58 ± 0.53), followed by Cape Campbell (3.54 ± 0.29) and lowest in Moeraki (1.74 ± 0.18), and associated with *C. retroflexa*, than *C. scalaris* and *C. torulosa* (Fig. 6.1E-H).

Gastropod community structure. The community structure was affected by several interactions, including the most complex 4-factor interactions but each significant interaction explained < 3% the data variability. In addition, all the individual test factors affected community structures, where Latitude explained most of the data variability (η^2 = 14%), followed by Reef (η^2 = 9.7%), secondary (η^2 = 2.4%) and primary habitat formers (η^2 = 1.5%). Visual inspection of the MDS plots (Fig. 6.2) showed in particular clear separation of the samples from Cape Campbell and Kaikoura, Kaikoura and Moeraki, and Cape Campbell and Moeraki.

6.4.2 Experiment 1: effects of primary and secondary habitat formers across seasons

Gastropod abundance. More than 18,000 gastropods were counted associated with the 65 collected fronds, represented by 49 morpho-species. Temperature and light levels were, on average, 12°C and 2402.7 Lux in winter and 17°C and 3269.2 Lux in summer. Two interactions were significant (Table 6.1). The interaction Season × 1st HF (p < 0.05, η^2 = 6.8%) showed that most gastropods were associated with *C. retroflexa*, followed by *C. scalaris* and *C. torulosa* (Fig. 6.3A) but mainly in the summer experiment. Additionally, more gastropods were found in the summer experiment compared to the winter experiment but only associated with *C. torulosa* and *C. retroflexa* (Fig. 6.3A-B). The second interaction, Season × 2nd HF (p < 0.05, η^2 = 5%), showed more gastropods in summer compared to winter on *Cystophora* without

epiphytes and on *Cystophora* with *Jania* (Fig. 6.3A). *Cystophora* fronds from the summer experiment were inhabited by more gastropods with than without epiphytes (SJ > SP > S, Fig. 6.3A) while, for *Cystophora* fronds from the winter experiment only, *Polysiphonia* epiphytes had more gastropods than non-epiphytised fronds (SP > S, Fig. 6.3B). All the single test factors were significant. Season explained most of the data variability (η^2 < 29%) with more than 2× more gastropods in summer than winter (Fig. 3A-B). The secondary habitat former explained ca 18% of the data variability, showing that *Cystophora* spp. with epiphytes were inhabited by more gastropods than without (Fig. 6.3A-B). Finally, 11% of the data variability was explained by primary habitat former identity showing that *C. retroflexa* and *C. scalaris* were inhabited by more gastropods than *C. torulosa* (Fig. 6.3A-B).

Gastropod richness. The 3-way 1st HF × 2nd HF × Season (Table 6.1) interaction was the only significant interaction (η^2 = 6.7%). However, all the single test factors were significant and Season explained most of the data variability (η^2 = 28.7%), follow by primary (η^2 = 11%) and secondary habitat former (η^2 = 7.3%). More taxa were found in winter than summer, on *C. scalaris* and *C. torulosa* than *C. retroflexa*, and associated with epiphytic *Polysiphonia* rather than *Jania* (and least on fronds without epiphytes, Fig. 6.3C-D).

Gastropod community structure. Community structure was significantly affected by Season (Table 6.1, η^2 = 22.3%) and secondary habitat former (η^2 = 6.2%) (Fig. 6.4). The MDS plots again showed clear separation between summer and winter samples but also that communities without epiphytes were different than with epiphytes (P = J ≠ 0, Fig. 6.4).

6.4.3 Experiment 2a: effects of secondary habitat former biomass and type across seasons (*C. scalaris*)

Gastropod abundance. More than 38,000 gastropods, representing 48 morpho-species, were counted on the 74 collected fronds.

The only significant interaction was Reef × 2nd HF Type (Table 6.1, p = 0.001, η^2 = 16.3%). This interaction suggested that more gastropods were associated with *Cystophora* fronds with mimic epiphytes in South Bay than Wairepo reef, and on *Cystophora* with living epiphyte compared to epiphytic mimics at Wairepo reef (Fig. 6.5A). Among the significant single test factors, Season and 2nd HF Biomass explained 12% and 5% of the data variability,

respectively, showing more gastropods in summer than winter, and on fronds with large than small epiphytic biomass (Fig. 6.5A).

Gastropod richness. As for abundance, the interaction Reef × 2nd HF Type was the only significant interaction (Table 6.1, $\eta^2 > 5\%$). However, all single factors effects were significant, where 2nd HF Type explained most of the data variability ($\eta^2 = 50\%$), followed by Season ($\eta^2 = 15.3\%$) and 2nd HF Biomass ($\eta^2 = 9.5\%$). More specifically, there were more taxa associated with living than mimic epiphytes, in summer than winter, and with low than high epiphyte biomass (Fig. 6.5B).

Gastropod community structure. I found two significant interactions (Table 6.1) explaining < 6% data variability each (Season × Reef and Reef × 2nd HF Type). Of the significant single factor effects, Season, again, explained most data variability (13%), followed by Reef ($\eta^2 = 10.8\%$) and 2nd HF Type ($\eta^2 = 3\%$). These results are shown on the MDS plot, where summer and winter samples were clearly separated (Fig. 6.6).

6.4.4 Experiment 2b: effects of secondary habitat former biomass and type (*H. banksii*)

Gastropod abundance. More than 7,000 gastropods representing 19 morpho-species were counted in the 33 frond samples.

The most important test factor was Reef ($p = 0.001$, Table 6.1, $\eta^2 = 26.3\%$), showing more gastropods in samples from South Bay than Wairepo reef. There was also a significant effect of 2nd HF Biomass with more gastropod inhabiting high than low epiphyte biomass (Fig. 6.5A).

Gastropod richness. There were no significant effects on richness (Table 6.1), although there was a tendency for more taxa being found in samples with live epiphytes (Fig. 6.5B).

Gastropod community structure. All the single test factors were significant (Table 6.1), where Reef explained most of the data variability ($\eta^2 = 25\%$), followed by 2nd HF Biomass (13.2%) and 2nd HF Type (8.8%). The MDS ordination showed *C. scalaris* and *H. banksii* samples as two distinct groups with a slightly less clear superimposed separation between samples of hosts with and without epiphytes (Fig. 6.6).

6.4.5 Comparison between *C. scalaris* and *H. banksii* (Experiment 2a-2b)

Gastropod abundance. The most important significant interactions were Reef × 2nd HF Type (Table 6.1, $\eta^2 > 15\%$) and Reef × 1st HF identity ($\eta^2 = 2.8\%$). These interactions showed that the strength, but not direction, of effects varied between South Bay and Wairepo reef (Fig. 6.5A). Of the significant single factor effects, primary habitat former identity explained most data variability ($\eta^2 = 21.5\%$), followed by Reef ($\eta^2 = 9.1\%$) and 2nd HF Biomass ($\eta^2 = 7.1\%$), revealing more gastropods on *C. scalaris* than *H. banksii* (95.25 ± 8.38 ind. / gDW 1st+2nd HF vs 44.79 ± 7.82) and on epiphytes with high than low biomass (97.32 ± 11.89 vs 64.46 ± 7.87, Fig. 6.5A).

Gastropod richness. The 1st HF × 2nd HF Type ($\eta^2 = 17.4\%$) and 1st HF × 2nd HF Biomass ($\eta^2 = 8.1\%$) interactions were both significant (Table 6.1). These interactions suggested that more taxa inhabited living epiphytes than mimics and high epiphytic biomass than low, but particularly when the host was *C. scalaris* (Fig. 6.5B). In addition, 2nd HF Type ($\eta^2 = 22.3\%$) and 1st HF identity ($\eta^2 = 12.1\%$) were also significant showing that living epiphytes hosted more taxa compared to mimics (2.95 ± 0.24 taxa / gDW 1st+2nd HF vs 2.21 ± 0.10), and *C. scalaris* more than *H. banksii* (2.75 ± 0.21 vs 2.34 ± 0.14) (Fig. 6.5B).

Gastropod community structure. There were two significant interactions (Reef × 1st HF, $p = 0.001$, and Reef × 2nd HF Type $p < 0.05$, Table 6.1) but they explained little of the data variability (combined ca 5%). The most important significant single factor effect was 1st HF ($\eta^2 > 40\%$), followed by Reef ($\eta^2 < 5\%$) and 2nd HF Type ($\eta^2 < 2\%$). This MDS plots showed clear separation of gastropod communities between the two seaweed hosts (Fig. 6.6).

6.4.6 Correlations

There were significant correlations between the biomass of both the primary and secondary habitat formers and both gastropod abundance ($r_{Spearman} = 0.51$ and $r_{Spearman} = 0.54$ respectively, $p < 0.001$, Fig. 6.7A-B) and taxonomic richness ($r_{Spearman} = 0.25$ and $r_{Spearman} = 0.59$ respectively, $p < 0.001$, Fig. 6.7C-D).

6.4.7 Experiment 3: effects of grazing

There were no significant effects of either Grazing or Season (Table 6.1, Fig. 6.8), which suggests that these small gastropods, at this particular density, either do not feed on the

seaweeds or that their grazing impact is very small. Video recording revealed that ca 50% of the snails were found out of the water (on the side of the cages), 20% in the water but not on seaweeds and only 30% were generally actively crawling (grazing) on the seaweeds.

6.4.8 Morphological traits of habitat formers

All morphological attributes of the primary and secondary habitat formers (surface area:dry weight, fractal dimension, circularity and lacunarity) were statistically significant ($p = 0.001$, Fig. 6.9-6.10). Pair-wise comparisons showed significant differences for all the morphological traits between *C. retroflexa* and the two congeneric species and between all *Cystophora* spp. and *H. banksii* (Fig. 6.9-6.10). Strong differences were also found between the three living epiphytes (*Jania* vs *Polysiphonia, Jania* vs *Notheia*, and *Polysiphonia* vs *Notheia*, $p < 0.004$) and between the artificial mimic and all the epiphytes (mimic vs *Polysiphonia*, mimic vs *Jania* and mimic vs *Notheia*, $p < 0.002$). In general, most primary habitat formers were different from most secondary habitat formers.

6.5 DISCUSSION

My results demonstrated that morphological similar and phylogenetic related co-occurring congeneric *Cystophora* species, can support different gastropod communities. I also found that latitudinal effects were relatively weak, seasonal effects strong, and, importantly, that secondary habitat-forming epiphytes facilitated gastropods both as living and mimic epiphytes, and that these habitat cascades arising from *Cystophora*-epiphyte interactions are widespread in space and time.

6.5.1 Biomass-standardized gastropod data

In this chapter, all gastropod data were standardised by the combined biomass of the host and epiphytes. This approach contrast many other habitat cascade studies that report results per sampled area (e.g., quadrat) (Altieri et al. 2010, Angelini and Silliman 2014, Bishop et al. 2013, Hughes et al. 2014) or standardised by the biomass of the primary (Thomsen et al. 2016b) or secondary (Buzá-Jacobucci and Pereira-Leite 2014) habitat former. The advantage of standardizing data by the total seaweed biomass is that it enables a more direct test of whether the secondary habitat former is a ‘better’, ‘equivalent’ or ‘worse’ habitat than the primary habitat former (i.e., if the biodiversity is higher, equal or lower in the presence of the epiphyte).

The disadvantage is, however, that this is a conservative approach that makes it less obvious if and when secondary epiphytes facilitate inhabitants.

6.5.2 Effects of primary habitat formers

In contrast to my hypothesis, congeneric and morphologically relatively similar *Cystophora* species affected epifauna differently. However, these results support Bates (2009), who also found that invertebrate communities can vary between closely related seaweed species. More gastropods were generally associated with *C. retroflexa* and *C. scalaris* compared to *C. torulosa,* perhaps because *C. torulosa* has slightly lower morphological complexity (e.g., lower surface area:dry weight ratio and lacunarity). Even more pronounced were the differences between the morphologically different *C. scalaris* and *H. banksii*, where the more complex *C. scalaris* was inhabited by many more gastropods than the simpler *H. banksii*. It has been shown in many studies that habitat formers with different morphologies typically are inhabited by different epifaunal assemblages (Cacabelos et al. 2010, Colman 1940, Gestoso et al. 2012, Seed and O'Connor 1981, Taylor and Cole 1994), including rocky shore gastropods (Beck 1998, 2000, Chemello and Milazzo 2002, Gestoso et al. 2012, Kostylev et al. 1997). Such differences have mainly been attributed to habitat structures (Beck 2000, Bell et al. 1991, Christie et al. 2007, Hauser et al. 2006, Johnson and Scheibling 1987, Menge and Lubchenco 1981, Tuya et al. 2011), where the structurally more complex seaweeds typically are inhabited by more diverse assemblages compared to less complex seaweeds (Chemello and Milazzo 2002, Hauser et al. 2006, Hicks 1985).

6.5.3 Effects of secondary habitat formers

As expected, the secondary habitat former (epiphyte) had a strong positive effect as *Jania* and *Polysiphonia* doubled the amount of gastropods on *Cystophora* (even after accounting for the biomass of the epiphytes). This result supports finding from Martin-Smith (1993), Pavia et al. (1999), Thomsen et al. (2016b) and Armitage and Sjøtun (2016), who also found more invertebrates when rocky shore habitat-forming seaweeds (*Sargassum* spp., *A. nodosum*, *H. banksii,* the two species *Fucus serratus* and *Codium fragile*, respectively) were epiphytised. Indeed, facilitation arising from multiple co-occurring habitat formers has also been documented from other ecosystems such as mangroves, saltmarshes and forests (Bishop et al. 2012, Callaway et al. 2001, Cruz-Angòn and Greenberg 2005, Dijkstra et al. 2012, Hughes et al. 2014, Stuntz et al. 2003). The morphological trait analysis may, in part, explain how gastropods are being facilitated by epiphytes, because epiphytes add different, typically more

complex habitat, to the primary habitat former, and thereby also add more and new niches for invertebrates to occupy (Buzá-Jacobucci and Pereira-Leite 2014, Martin-Smith 1993, Pavia et al. 1999). Evidence of these habitat cascades were generally found across latitudes, reefs and season suggesting they are general processes, not only across habitats and ecosystems but also across a wide range of spatio-temporal and environmental conditions (Angelini and Silliman 2014, Angelini et al. 2015, McAfee et al. 2016, Thomsen et al. 2010).

6.5.4 Effects of secondary habitat former biomass and type

Results from the second experiment provided additional insights into the role of secondary habitat formers as epiphyte biomass was positively related to gastropod abundances and richness. This result was supported by my more general correlation analysis carried out across all my survey and experimental data. Several studies have found similar positive correlations with epiphytic biomass and biodiversity (Colman 1940, Edgar 1983, Gunnill 1982, 1983, Hagerman 1966, Kangas 1978, Nagle 1968, Zavodnik 1967), typically attributing increasing facilitation with increasing epiphyte biomass to increasing amount and complexity of habitat and more food resources (Buzá-Jacobucci and Pereira-Leite 2014, Parker et al. 2001, Wikström and Kautsky 2004, Worm and Sommer 2000). Epiphyte type (i.e., whether epiphytes were alive or not) did not statistically affect gastropod abundances (but slightly more taxa were found on live than non-living epiphytes). This result suggests that the majority of taxa mainly benefit from the structure provided by the epiphyte more than the trophic subsidy. Other studies have also shown that artificial epiphytes can provide comparable habitat to living epiphytes (Hall and Bell 1988, Martin-Smith 1993). However, it is unclear if invertebrate colonization of these artificial types of substrates is caused by active behavioural choices or passive convergence toward the mimics (Dean and Connell 1987).

6.5.5 Effect of latitude and season

It has previously been shown that facilitation from intertidal biogenic habitats can be stronger at warmer more stressful low latitudes (McAfee et al. 2016). I therefore expected to find more gastropods associated with biogenic habitats at northern reefs, as gastropods may be exposed to more stressful conditions there (Davison and Pearson 1996, McAfee et al. 2016), including high temperature (Cole 2010, Silliman et al. 2011). I did find significant effects of latitude but with any clear latitudinal gradient in gastropod responses. This results support studies on tree epiphytes (Angelini and Silliman 2014) and mussels in saltmarshes (Angelini et al. 2015), where there were no clear latitudinal patterns in facilitation of invertebrates. However, I

generally did find higher abundances and more taxa associated with biogenic habitats in summer compared to winter suggesting (i) a phenological variation in recruitment dynamics (Mieszkowska et al. 2006, Moore et al. 2011), (ii) that biogenic habitats are more important buffers of environmental stress during warmer months (McAfee et al. 2016), and/or (iii) a different response to seasonal fluctuation of food availability (Taylor 1997). These results contrast with Cowles et al. (2009), who did not find seasonal effects on invertebrate distribution pattern, represented mainly by gastropods, in New Zealand intertidal rocky reefs.

6.5.6 Effects of grazing

Results from the grazing experiment suggest that gastropods either do not consume seaweeds or that consumption rates are below detection levels from this typical ecological experiment. Instead, gastropods may inhabit seaweeds to avoid predation (Beck 1998, Yamada and Boulding 1996), reduce physiological stress (Beck 1998), or find other resources, for example if they feed on microscopic biofilms (Simental et al. 2004, Steneck and Watling 1982). Indeed, Arrontes (1999) suggested that most epifaunal species do not consume their host. These explanations are also supported by studies that have shown that abiotic mimics are rapidly colonized by small mobile invertebrates (this study, Hall and Bell 1988, Martin-Smith 1993). Nevertheless, it has been demonstrated that some gastropods do graze on epiphytes (D'Antonio 1985, Jaschinski and Sommer 2008, Nielsen and Lethbridge 1989) and many other studies have shown how small invertebrates utilize their biogenic habitat as a trophic resource (Buzá-Jacobucci and Pereira-Leite 2014, D'Antonio 1985, Duffy 1990, Nicotri 1980, Pavia et al. 1999, Taylor and Steinberg 2005). The most likely reason for the discrepancy between these grazing studies and my experiment is likely that the natural grazing densities used here are simply too low to limit the seaweeds (Duffy et al. 2005).

6.5.7 Conclusions

Many studies have demonstrated how different seaweed species with widely different morphological complexities modify epifaunal communities. My results add to these studies by showing that even minor differences in morphology support significantly different faunal communities. It is therefore important to improve our ability to quantify these morphological attributes (Veiga et al. 2014) and my findings suggest that further analysis on seaweed structural complexity are needed in order to find a unique, univocal and quantitative measure to discriminate the morphological difference among seaweed species.

Tables

Table 6.1 Overview of PERMANOVA reporting the results of the factorial analysis. All factors were treated as fixed and 'Reef' was nested in 'Latitude'. Values represent the contribution of each test factor to the total variability of the PERMANOVA models ($\eta^2 = SS_{Explained}/SS_{Total}$). Univariate and multivariate variables were analyzed with Euclidean distance and Bray-Curtis similarity coefficient, respectively. See Appendix 3-6.4, 3-6.5, 3-6.6, 3-6.7, 3-6.8 and 3-6.9 for complete PERMANOVA tables. Significant values are in bold (*: p = 0.05-0.01, **: p = 0.01-0.001, ***: p < 0.001).

Factors	Abundance	Richness	Community structure	% lost biomass
Spatial survey: effects of primary and secondary habitat formers across latitudes				
Latitude (Lat)	**6.66%*** **	**20.53%*** **	**14.53%*** **	
1st HF (1HF)	**6.32%*** **	**3.19%***	**1.49%*** **	
2nd HF (2HF)	**7.85%*** **	0.40%	**2.36%*** **	
Reef(Latitude) Ree(Lat)	**9.15%*** **	**9.79%*** **	**9.66%*** **	
Lat × 1HF	2.19%	3.13%	**2.96%** **	
Lat × 2HF	0.32%	0.12%	**2.32%*** **	
1HF × 2HF	0.95%	0.56%	0.80%	
Ree(Lat) × 1HF	**3.95%***	0.94%	2.39%	
Ree(Lat) × 2HF	2.01%	**3.24%***	**2.42%*** **	
Lat × 1HF × 2HF	**3.30%***	0.92%	1.86%	
Ree(Lat) × 1HF × 2HF	1.96%	0.73%	**2.57%***	
Experiment 1: effects of primary and secondary habitat formers across seasons				
Season (Sea)	**28.59%*** **	**28.74%*** **	**22.28%*** **	
1st HF (1HF)	**10.84%** **	**11.01%** **	2.73%	
2nd HF (2HF)	**17.77%*** **	**7.32%** **	**6.22%*** **	
Sea × 1HF	**6.82%***	3.58%	2.11%	
Sea × 2HF	**4.98%***	2.92%	3.04%	
1HF × 2HF	1.68%	2.66%	3.78%	
Sea × 1HF × 2HF	5.33%	**6.69%***	3.53%	
Experiment 2a: effects of secondary habitat former biomass and type across seasons (*C. scalaris*)				
Season (Sea)	**12.14%** **	**15.32%*** **	**12.92%*** **	
Reef (Ree)	2.25%	2.94%	**10.83%*** **	
2nd HF type (Typ)	3.59%	**48.45%*** **	**3.01%** **	
2nd HF biomass (Bio)	**5.53%***	**9.54%** **	1.57%	
Sea × Ree	0.03%	1.85%	**2.87%** **	
Sea × Typ	0.01%	1.66%	1.19%	
Sea × Bio	1.21%	2.16%	1.79%	
Ree × Typ	**16.28%*** **	**5.24%***	**2.85%***	
Ree × Bio	0.01%	2.41%	0.78%	
Typ × Bio	3.51%	0.03%	1.48%	
Sea × Ree × Typ	1.75%	1.00%	0.70%	
Sea × Ree × Bio	0.00%	2.40%	0.87%	

Sea × Typ × Bio	3.33%	0.11%	1.38%
Ree × Typ × Bio	0.01%	1.14%	0.94%
Sea × Ree × Typ × Bio	0.45%	0.01%	0.54%
Experiment 2b: effects of secondary habitat former biomass and type (*H. banksii*)			
Reef (Ree)	**26.34%*** **	1.41%	**25.64%*** **
2nd HF type (Typ)	0.72%	0.55%	**8.76%** **
2nd HF biomass (Bio)	**18.82%*** **	1.06%	**13.22%** **
Ree × Typ	4.26%	0.80%	5.42%
Ree × Bio	4.96%	0.26%	2.02%
Typ × Bio	0.77%	0.10%	4.72%
Comparison between *Cystophora scalaris* and *Hormosira banksii* (Experiment 2a-2b)			
Reef (Ree)	**9.14%** **	1.46%	**4.81%*** **
1st HF (1HF)	**21.49%*** **	**12.11%** **	**41.97%*** **
2nd HF type (Typ)	0.76%	**22.29%** **	**1.77%%***
2nd HF biomass (Bio)	**7.14%** **	4.28%	1.48%
Ree × 1HF	**2.83%***	4.41%	**3.49%*** **
Ree × Typ	**15.18%*** **	2.07%	**1.64%***
Ree × Bio	0.00%	3.45%	0.86%
1HF × Typ	1.31%	**17.35%*** **	1.45%
1HF × Bio	1.94%	**8.06%***	1.03%
Typ × Bio	0.31%	0.04%	0.47%
Ree × 1HF × Typ	2.47%	4.44%	0.76%
Ree × 1HF × Bio	0.04%	2.19%	0.67%
Ree × Typ × Bio	2.56%	0.56%	0.49%
1HF × Typ × Bio	0.36%	0.00%	0.72%
Ree × 1HF × Typ × Bio	0.99%	0.08%	0.80%
Laboratory grazing experiment			
Grazers (Gra)			0.10%
2nd HF (2HF)			**13.06%*** **
1st HF (1HF)			**5.83%***
Season (Sea)			0.03%
Gra × 2HF			1.34%
Gra × 1HF			2.38%
Gra × Sea			0.45%
2HF × 1HF			**7.21%***
2HF × Sea			1.40%
1HF × Sea			3.57%
Gra × 2HF × 1HF			5.88%
Gra × 2HF × Sea			0.18%
Gra × 1HF × Sea			1.34%
2HF × 1HF × Sea			3.77%
Gra × 2HF × 1HF × Sea			3.02%

Figures

Figure 6.1 Spatial survey, effects of primary and secondary habitat formers across latitudes. Abundance (A-D) and richness (E-H) of gastropods associated with three congeneric primary habitat-forming seaweeds (*Cystophora retroflexa*, *C. scalaris*, *C. torulosa*) with and without attached secondary habitat-forming epiphytes collected at Cape Campbell (A, E), Kaikoura (B, F), Pile Bay (C, G) and Moeraki (D, H). Data were standardized by dry weight of the total association of habitat-forming species (primary + secondary habitat former). Error bars = 1 SE, n = 8. The test factor 'Reef' was pooled. There is no error bar for samples with no replicates. See Appendix 3-6.1 for data relative to the samples without associated epiphytes and Appendix 3-6.4 for statistical analyses. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'latitude' test factor, lower case letters to the 'primary habitat former' test factors.

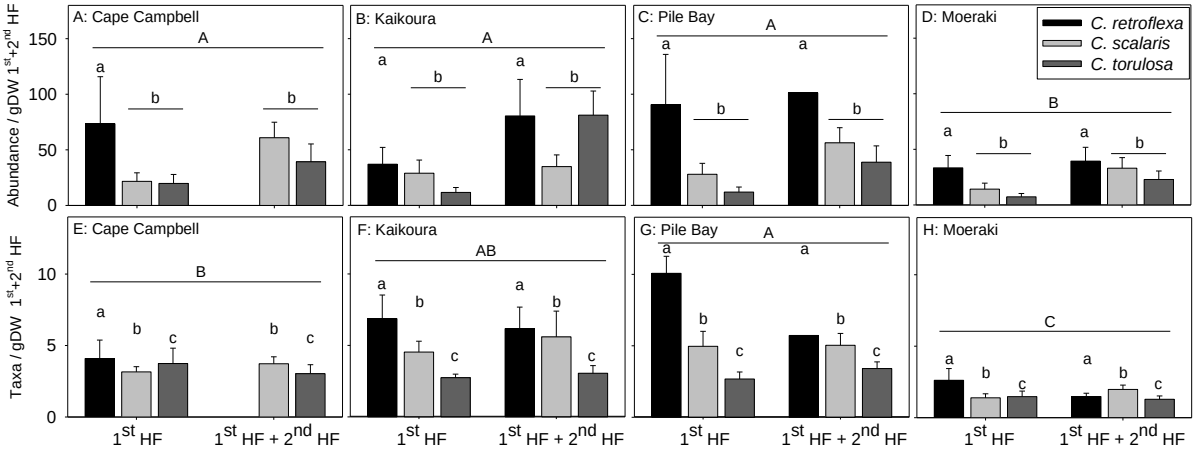


Figure 6.2 Spatial survey, effects of primary and secondary habitat formers across latitudes. MDS plot of community structure (based on Bray-Curtis similarity) for three primary habitat formers (R: *Cystophora retroflexa*, S: *C. scalaris*, T: *C. torulosa*) with (+) and without (-) epiphytes. For simplicity, data were split into four locations but results are from the same analysis and the plots can be superimposed on each other (and therefore have the same taxa vectors). n = 8. Data were square-rooted. Stress: 0.24.

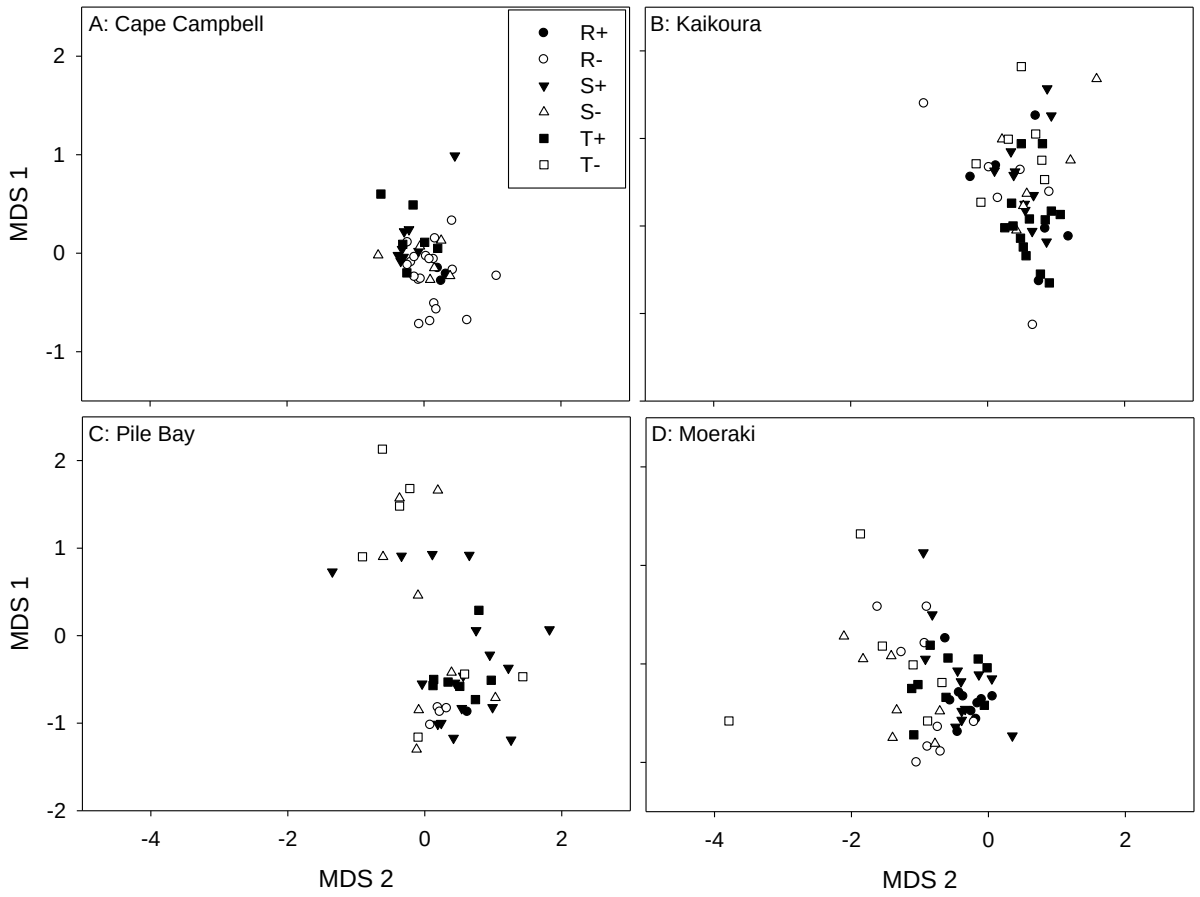


Figure 6.3 Experiment 1, effects of primary and secondary habitat formers across seasons. Abundance (A, B) and richness (C, D) of gastropods in three congeneric primary habitat formers (*Cystophora retroflexa, C. scalaris, C. torulosa*) with and without epiphytes (J: *Jania micrarthrodia*, P: *Polysiphonia decipiens*) in summer (A, C) and winter (B, D). Data were standardized by dry weight of the total seaweed association. Error bars = 1 SE, n = 4. There is no error bar for samples with no replicates. See Appendix 3-6.5 for statistical analyses. Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'secondary habitat former' test factor, lower case letters to the 'primary habitat former' test factors.

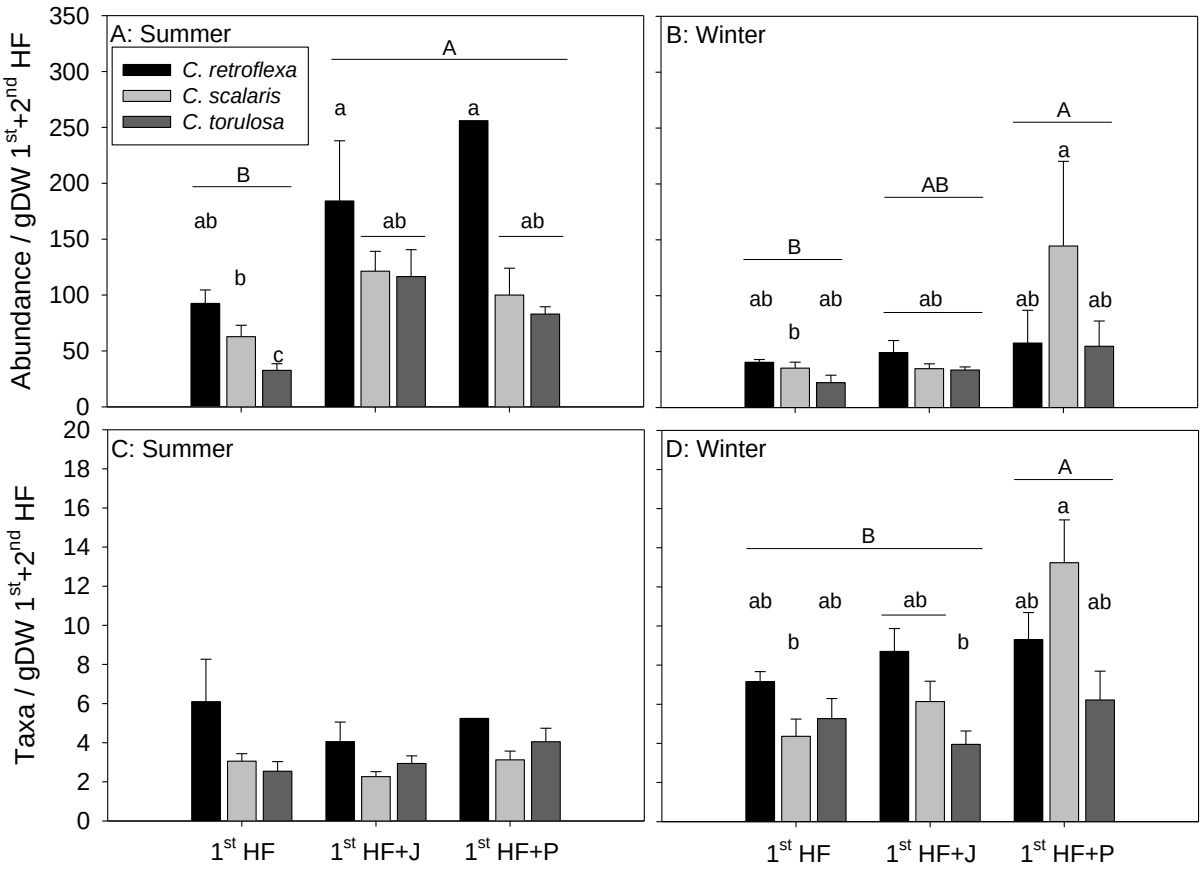


Figure 6.4 Experiment 1, effects of primary and secondary habitat formers across seasons. MDS based on community structure (based on Bray-Curtis similarity) for three primary habitat formers (*Cystophora retroflexa*, *C. scalaris*, *C. torulosa*) with (+) and without (-) epiphytes (A) and for three different epiphyte levels (B; 0: no epiphyte, J: *Jania micrarthrodia*, P: *Polysiphonia decipiens*). Plot A, n = 12; Plot B, n = 24. Data were square-root transformed prior to analysis. Stress: 0.20.

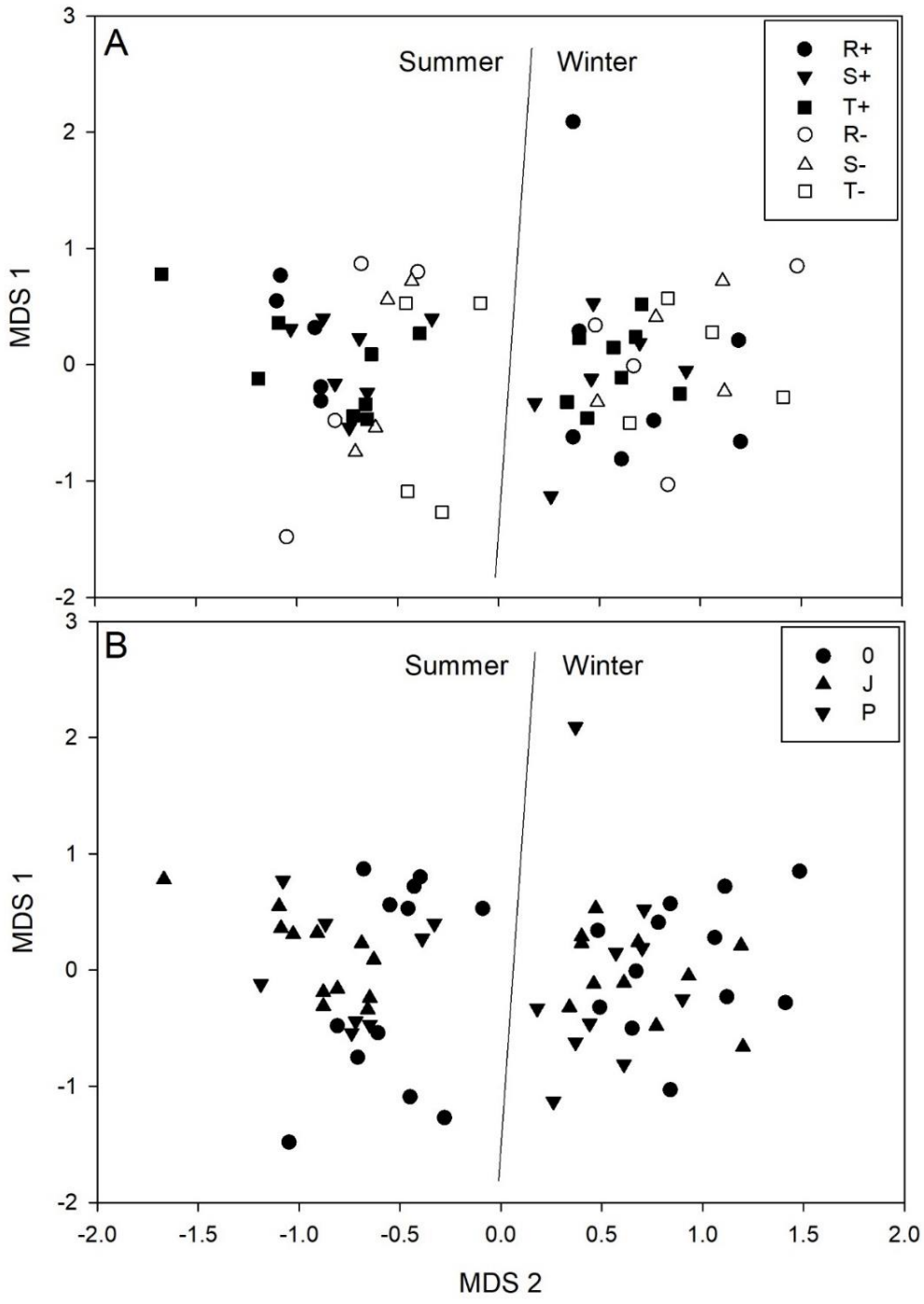


Figure 6.5 Experiment 2, effects of secondary habitat former biomass and type on *Cystophora scalaris* and *Hormosira banksii*. Abundance (A) and richness (B) of gastropods in the two different primary habitat formers without (0) and with living (L) and non-living mimic (M) epiphytes in both low (1) and high (2) biomasses. The living epiphyte were *Polysiphonia decipiens* and *Notheia anomala* for *C. scalaris* and *H. banksii*, respectively. Data were standardized by the dry weight of the total seaweed association. The control treatment without epiphytes (0, n = 4) was not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. Error bars = 1 SE, n = 4. The test factor 'Reef' was pooled. See Appendix 3-6.6 and 3-6.7 for statistical analyses Different letters indicate significant differences as detected by pair-wise t-test comparisons. Capital letters refers to the 'secondary habitat former type' test factor, lower case letters to the 'secondary habitat former biomass' test factors.

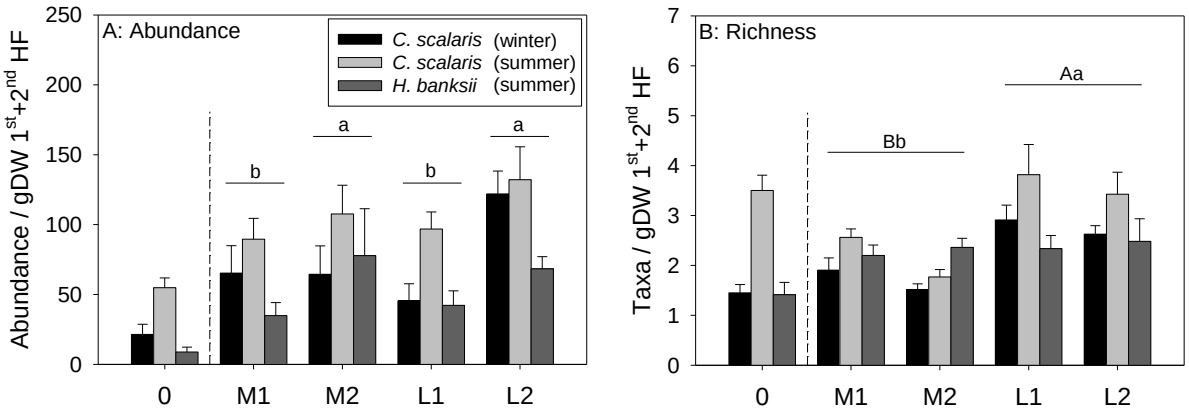


Figure 6.6 Experiment 2, effects of secondary habitat former biomass and type on *Cystophora scalaris* and *Hormosira banksi*. MDS plots of gastropod community structures associated with two different primary habitat formers (SS = *Cystophora scalaris* in summer, WS = *C. scalaris* in winter, SH = *Hormosira banksii* in summer) without (0) and with living (L) and non-living mimic (M) epiphytes in low both (1) and high (2) biomasses (based on Bray-Curtis similarity). The living epiphyte were *Polysiphonia decipiens* and *Notheia anomala* for *C. scalaris* and *H. banksii*, respectively. n = 8. Data were square-root transformed prior to analysis. Stress: 0.14.

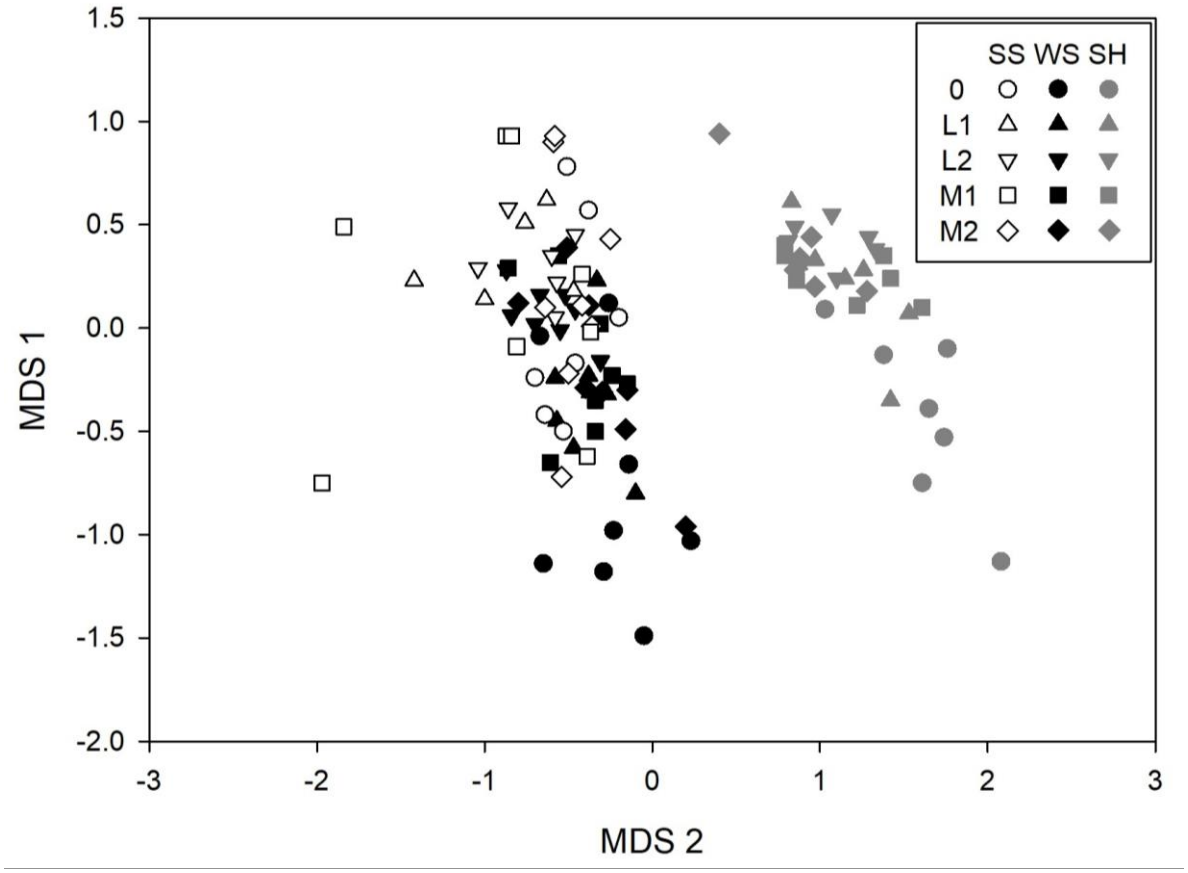


Figure 6.7 Correlation between the biomass of the primary (*Cystophora retroflexa*, *C. scalaris*, *C. torulosa*, *Hormosira banksii*) and secondary (*Jania micrarthrodia*, *Polysiphonia decipiens*, *Notheia anomala*, mimic) habitat formers in relation to the abundance (A, B) and taxonomic richness (C, D) of gastropods. Survey: n = 189, Experiment 1: n = 72, Experiment 2a: n = 80, Experiment 2b: n = 40. Outliers removed on graphs for clarity: A: 43.17 gDW vs 9028 gastropods (survey), D: 13.45 gDW vs 33 taxa (survey). r = Spearman's rank correlation coefficient; all correlations were significant ($p < 0.001$).

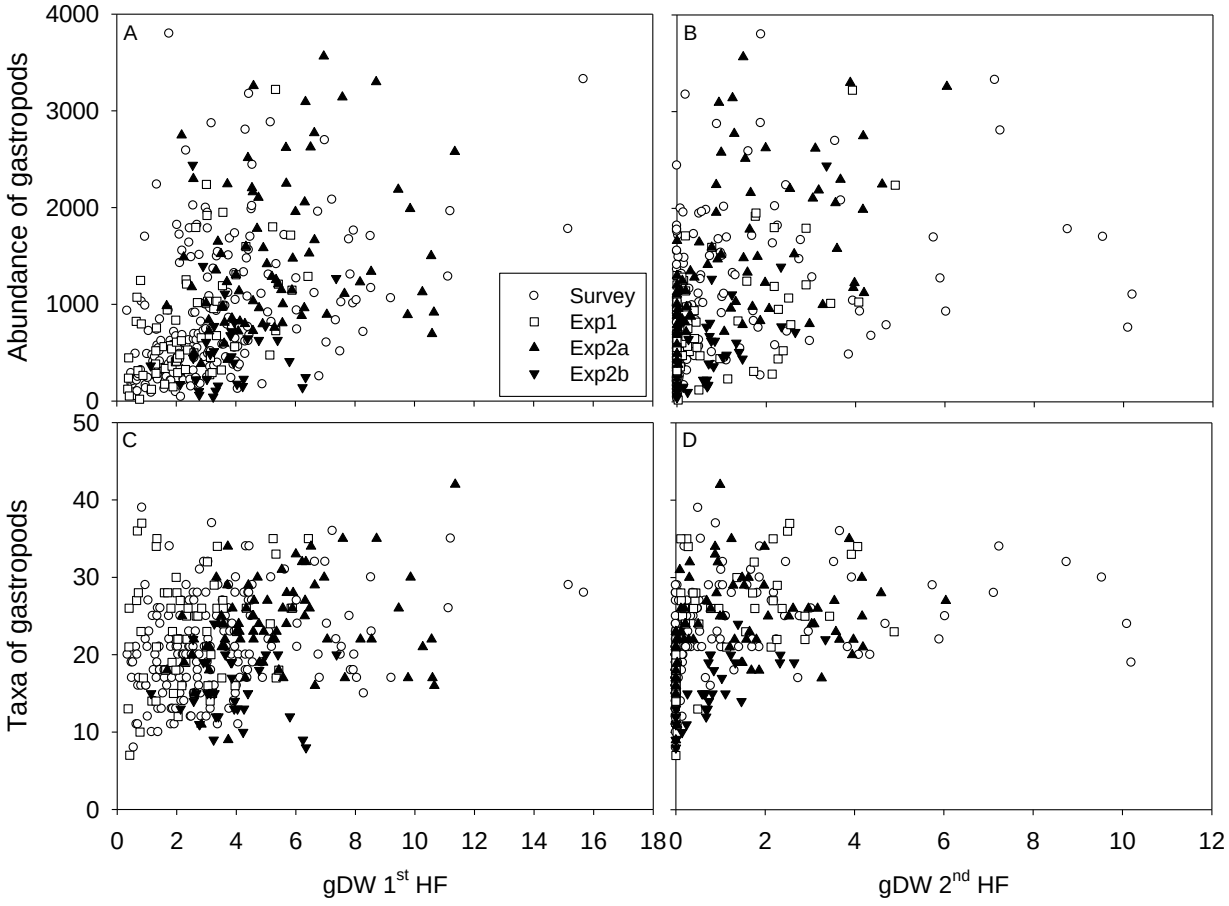


Figure 6.8 Laboratory grazing experiment. Percentage of seaweeds lost biomass in the 'summer' (A) and 'winter' (B) experimental simulations. R: *Cystophora retroflexa*, S: *C. scalaris*, T: *C. torulosa*, J: *Jania micrarthrodia*, P: *Polysiphonia decipiens*. Error bars = 1 SE, n = 3.

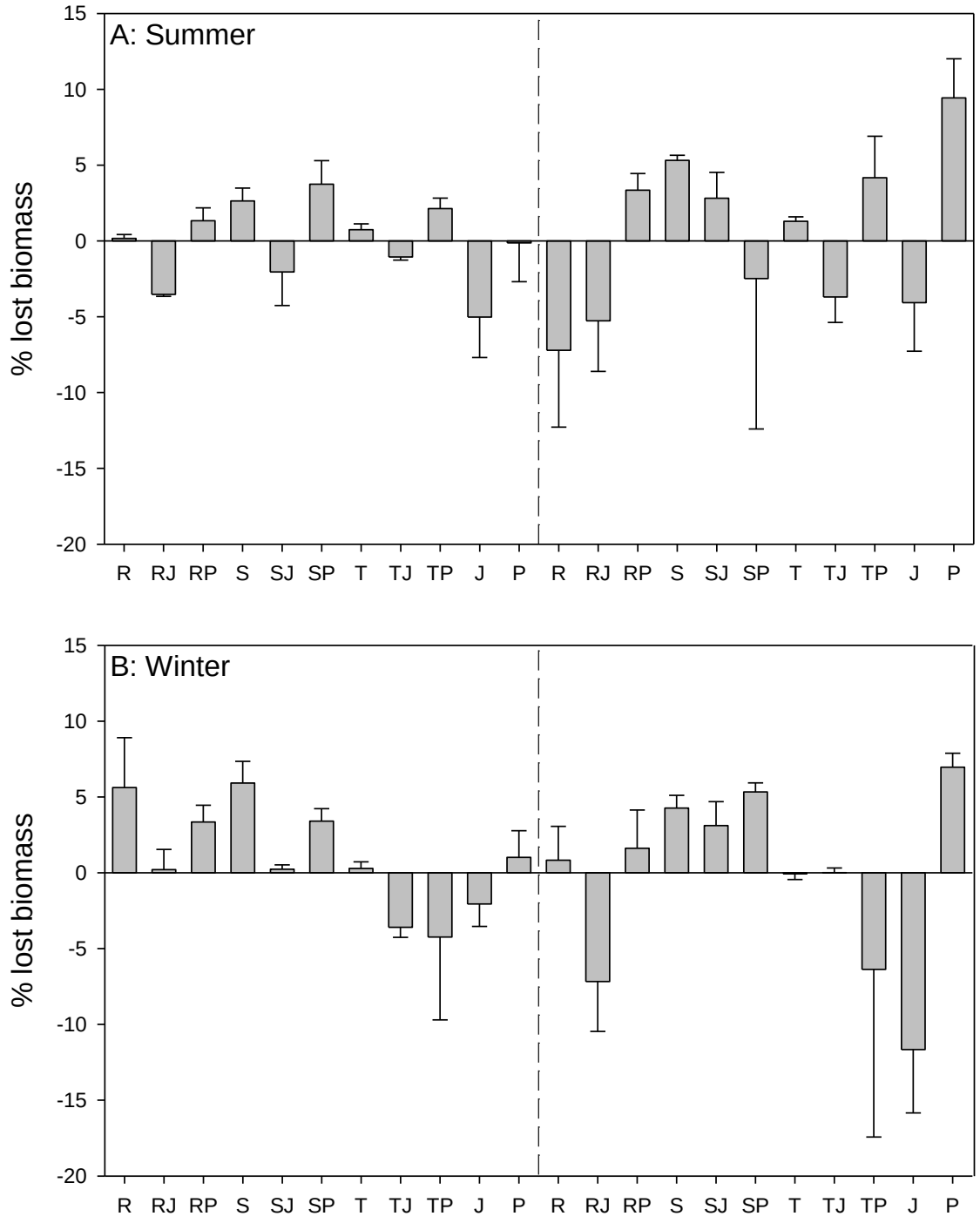


Figure 6.9 PCO analysis of morphological traits of primary (*Cystophora retroflexa*, *C. scalaris*, *C. torulosa*, *Hormosira banksii*) and secondary (*Jania micrarthrodia*, *Polysiphonia decipiens*, *Notheia anomala*, epiphyte mimic) habitat formers. n = 15 for primary habitat formers, n = 10 for secondary habitat formers. SDw: surface area:dry; Db: fractal dimension; C: circularity; Λ: lacunarity. Data were square-rooted and normalised prior to analysis.

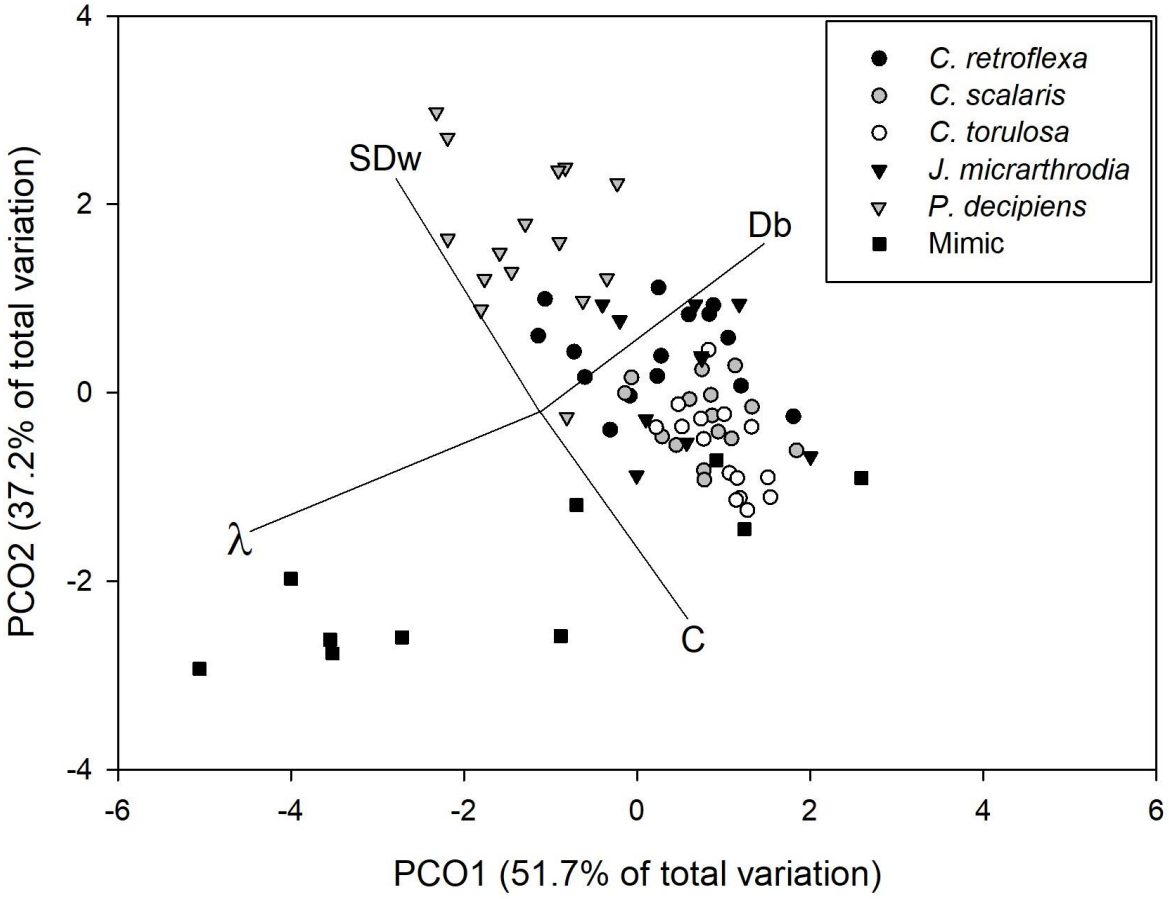
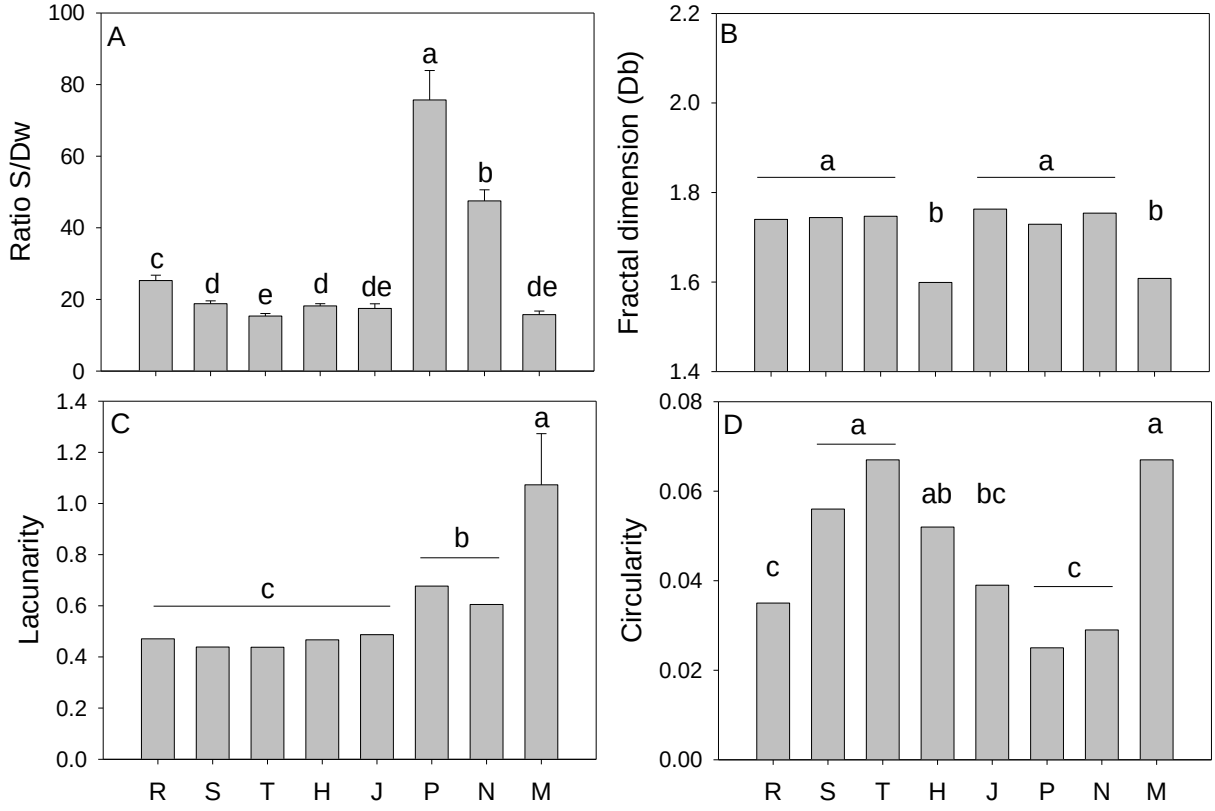


Figure 6.10 Morphological traits of primary (R: *Cystophora retroflexa*, S: *C. scalaris*, T: *C. torulosa*, H: *Hormosira banksii*) and secondary (J: *Jania micrarthrodia*, P: *Polysiphonia decipiens*, N: *Notheia anomala*, M: epiphyte mimic) habitat formers. Error bars = 1 SE, n = 15 for primary habitat formers, n = 10 for secondary habitat formers. In most of cases, error bars are too small to be visible. Different letters indicate significant differences as detected by pair-wise t-test comparisons.



CHAPTER 7: Effects of host and epiphyte traits, latitude, and season on secondary production in rocky shore facilitation cascades

7.1 ABSTRACT

Numerous studies have quantified how co-occurring habitat-forming species affect population abundances and diversity of animal communities. However, little is known about effects on other ecosystem functions such as the production of animal biomass. Here, I estimated secondary production of small mobile invertebrates living on intertidal seaweed, by combining the size and abundance of seaweed-associated animals with temperature data. More specifically, I tested if (i) three coarsely branched *Cystophora* species support similar secondary production, as similar morphological species should support similar fauna, (ii) presence of co-occurring finely branched epiphytes increase secondary production, as these structures should be inhabited by more invertebrates than coarsely branched species, (iii) production is greatest in northern locations and in warm seasons, as higher temperature often enhances production, (iv) secondary production is higher in living than non-living epiphytes, as biogenic habitat should provide both physical protection and a trophic resource, and (v) production is driven by crustaceans and molluscs, typically the most abundant small mobile marine animals. The first three hypotheses were tested by collecting the three *Cystophora* species with and without epiphytes across a latitudinal gradient, and a field experiment, where two epiphytic species were added to each of the three host species. The first hypothesis was rejected because both the survey and the experiment showed different secondary production between the morphologically similar host species. Similarly, both survey and experimental data rejected the second hypothesis; epiphytes, when its biomass was taken into consideration, did not increase secondary production. However, the third hypothesis was supported because production peaked in the northern location and in summer months, the former results driven more by regional differences in temperatures than differences in invertebrate abundances. The fourth hypothesis was investigated in a second field experiment, where artificial and living epiphytes were transplanted to the *C. scalaris*. Results from this experiment demonstrated, as expected, higher secondary production in the presence of living than mimic epiphytes, and confirmed higher production in summer compared to winter. Finally, the last hypothesis was tested across survey and experimental data, confirming that crustaceans and molluscs largely

control secondary production. I conclude, based on counts, identifications and size estimations of 339,671 invertebrates, that (i) similar looking congeneric host species supported different secondary production and (ii) epiphytes did not increase secondary production per seaweed-biomass, but will nevertheless increase areal-based production when and where epiphytes enhance total standing plant biomass. Finally, I suggest that future studies estimate secondary production in facilitation cascades from other habitats, like forests, mangroves, seagrass beds and estuaries, to test the generality of my results across ecosystems and scales.

7.2 INTRODUCTION

Facilitation cascades describe processes whereby sequential biogenic habitat formation or modification alters communities of habitat-associated organisms (Altieri et al. 2007, Thomsen et al. 2010). Facilitation cascades have been reported from marine, freshwater and terrestrial ecosystems and are particularly common where epiphytes are ubiquitous such as in forests, seagrass beds, mangroves and on rocky shores (Angelini and Silliman 2014, Cruz-Angòn et al. 2009, Cruz-Angòn and Greenberg 2005, Hall and Bell 1988, McAfee et al. 2016, Watson and Herring 2012). Most facilitation cascade studies have described effects on the abundance, diversity and structure of animal communities (Thomsen et al. 2018). By contrast, little is known about how co-occurring habitat formers affect other ecosystem functions such as decomposition rates or secondary production (the generation of biomass of heterotrophic consumer organisms in a system) (but see Angelini et al. 2015). More specifically, I am only aware of one study where secondary production was compared between single and co-occurring habitat-forming species. In that study, Valentine and Heck (1993) found that mussels embedded within seagrass beds increased secondary production compared to seagrass without mussels, with the important implication that mussels not only increased biodiversity but also energy flow in seagrass beds.

The scarcity of studies estimating community-wide secondary production in facilitation cascades may be partly due to methodological difficulties compared to measuring animal abundances and diversity (Dolbeth et al. 2012, Thomsen et al. 2018). This is particularly relevant for rocky shore epifaunal communities, where the contribution of small mobile fauna to secondary production was long ignored, instead using either microorganisms or a few large conspicuous species (Miller et al. 1971, Newell et al. 1982, Taylor 1998a). Nevertheless, small mobile epifauna are ecologically important in benthic communities because they are highly abundant (Choat and Kingett 1982, Holbrook and Schmitt 1996, Taylor and Cole 1994), have

high metabolic rates (Edgar and Moore 1986), and provide food for predators, including commercially important fish and crustaceans (Edgar and Moore 1986, Holbrook et al. 1990, Jones 1988, Moreno and Jara 1984, Simenstad et al. 1977, Taylor 1998a). Estimation of secondary production for these faunal communities is complicated by their high diversity, cryptic appearance, and small sizes making it almost impossible to use cohort analysis (Taylor 1998a), a method that typically focuses on the few dominant large conspicuous species (Crisp 1984, Robertson 1984, Warwick and Price 1975). Instead, allometric models, that relate faunal taxonomy, abundances, sizes and ambient temperature conditions to secondary production (Dickie et al. 1987, Dolbeth et al. 2012, Edgar 1990c), could be particularly useful in facilitation cascades, which often are dominated by small inconspicuous and diverse epifaunal communities (Edgar and Robertson 1992, Hall and Bell 1988, Pavia et al. 1999, Thomsen et al. 2016b, Viejo and Åberg 2003).

Estimation of secondary production is a key component of ecological studies as an integrated measure of energy flow (Edmondson 1974, Waters 1977), which combines biotic and abiotic influences (Cusson and Bourget 2005), and emphasizes that animals are both consumers and nutrient recyclers (Taylor 1998a). In addition to temperature (Robinson et al. 1983), secondary production can be affected by sinking of organic matter (Honjo 1980, Pomeroy et al. 1984, Roman and Tenore 1984), organic content of sediments and flux of suspended particles (Edgar 1990a), and food availability (Edgar 1990c). Variation in production is expected across latitudes and seasons due to increased metabolic rates at higher temperatures (Bullock 1955, Clarke 1987, Longhurst and Pauly 1987). For example, production of marine invertebrates (Valentine and Heck Jr 1993), including crustacean (Bauer 1989, Sastry 1983) and bivalves (Mazé and Laborda 1988, Vakily 1990), has been documented to be higher at lower than higher latitudes. Similarly, production can be greater in spring and summer than winter, due to a combination of higher temperatures and greater food availability (Nakaoka 1992b).

In this study, secondary production was estimated for small mobile faunal communities inhabiting three congeneric and morphologically 'similar' coarsely branched seaweed hosts (*Cystophora retroflexa*, *C. scalaris*, and *C. torulosa*, here primary habitat formers), from intertidal rocky shores of the South Island of New Zealand. These species were collected with or without epiphytes (mainly the red seaweeds *Jania micrarthrodia* and *Polysiphonia decipiens,* here secondary habitat formers) from different latitudes and seasons. Production was estimated using Edgar's (1990c) allometric models for small mobile invertebrates inhabiting

marine plants in Australia (i.e., these models were developed from similar conditions to my model system).

The hypotheses tested were: (i) the three *Cystophora* species support similar secondary production because they are evolutionary and morphologically relatively similar (Appendix 1, Adams 1997, Buchanan 2011, Cavender-Bares et al. 2004); (ii) the presence of epiphytes increases secondary production because these epiphytes are evolutionary and morphologically more different from their hosts and thereby create more and different habitat space (Pavia et al. 1999, Thomsen et al. 2016b, Thomsen et al. 2010, Viejo and Åberg 2003); (iii) secondary production is greatest at northern latitudes and in summer because invertebrate production generally increases with increasing temperature (Edgar 1990c); (iv) secondary production is higher when epiphytes are alive instead of being non-living mimics, because the living habitat former provides both a physical structure and a trophic resource (whereas mimics provide only physical structure) (Bologna and Heck 1999, 2000, Gribben et al. 2017a, Macreadie et al. 2014); (v) production by crustaceans and molluscs exceed the production by other taxa such as polychaetes and caprellidae, as shown for invertebrates inhabiting other seaweeds in New Zealand rocky shores (Cowles et al. 2009, Taylor 1998a). The first three hypotheses were addressed with a spatial survey across four latitudes on the eastern coast of the South Island of New Zealand and with a field experiment that manipulated the abundances of two common epiphytes. The fourth hypothesis was tested with a second field experiment where the abundances of live and non-living plastic epiphyte-mimics were manipulated whereas the fifth hypothesis was examined graphically across all data collections (in part because the results were obvious, in part because the different taxonomic groups are not independent from each other thereby violating standard test assumptions). These analyses differ from other facilitation cascade studies (Thomsen et al. 2018) in two fundamental ways: (i) results are presented as secondary production instead of animal abundances, and (ii) results were standardized by the total biomass of the sampled habitat-forming seaweeds instead of per collected sample (typically reported per quadrat or core). To aid comparisons between my secondary production estimates and past facilitation cascade research, results were also tabulated based on standard reporting formats, showing animal abundances per sample (Table 7.2).

7.3 MATERIALS AND METHODS

7.3.1 Study region

The study was done in the rocky intertidal zone of the east coast of the South Island of New Zealand. Surveys were conducted on reefs at Cape Campbell (41°43'36.685"S, 174°16'31.962"E), Kaikoura (42°24'51.707"S, 173°42'18.472"E), Pile Bay in Lyttelton Harbour (43°37'16.126"S, 172°45'42.736"E) and Moeraki (45°21'31.907"S, 170°51'43.823"E). These reefs span a 4° latitudinal gradient, covering > 550 km coastline and have a temperature gradient of ca 3°C (mean annual SST = 11°C at Moeraki vs 14°C at Cape Campbell, Schiel 2011). The reefs from Cape Campbell, Kaikoura and Moeraki extend approximately 150 m from the upper intertidal to the subtidal zones and are generally protected from severe wave action by off-shore reefs and have a coastal topography that deflects swells (Ramage and Schiel 1999). In Pile Bay, the reef only extends ca 50 m and is located in the outer part of a protected large bay and are therefore also exposed to swell waves. The three northern reefs are part of the East Coast South Island biogeographic coastal zone whereas Moeraki is within the Southern South Island zone. All reefs were under the influence of the Southland Current and the lower intertidal platforms are dominated by the same canopy-forming seaweeds such as different *Cystophora* species (Schiel 2011). Sampling for the survey and the two field experiments was done in middle and low shore intertidal tide pools and channels during low tide.

7.3.2 Spatial survey: effects of primary and secondary habitat formers

Fronds were collected from three common *Cystophora* species (*C. retroflexa*, *C. scalaris* and *C. torulosa*) in summer, from November 2014 to February 2015. These species were collected with and without attached epiphytes. Collections were made at two reefs (> 500 m apart) within each of the 4 latitudes (> 100 km apart). At each reef, *Cystophora* species were collected from four tide pools or tidal channels (that is, all samples were submerged at the time of collection). Approximately 15 cm of fronds were cut off of each *Cystophora* species, with and without epiphytes, and quickly transferred to a sealed plastic bag to minimize loss of mobile invertebrates (Buschbaum et al. 2006, Gribben et al. 2009, Vázquez-Luis et al. 2012). Bags were stored in ice chests before being transported to the lab for processing. The sampling design was: 3 *Cystophora* species × 2 secondary habitat former levels (± epiphytes) × 4 latitudes × 2 reefs (within each latitude) × 4 replicated tide-pools/channels per reef (i.e., I aimed to collect 192 samples). However, there were a few reefs where some of the *Cystophora* species with

epiphytes were absent, resulting in a slightly unbalanced statistical test design. Furthermore, epiphytic species identity varied between reefs. The main epiphytes were the red algae *Jania micrarthrodia* and *Polysiphonia decipiens* (hereafter *Jania* and *Polysiphonia*), common on most reefs along the east coast of New Zealand (Adams 1997). On a few sampled reefs, however, these epiphytic species were absent from *Cystophora*, so host fronds with different epiphyte species were collected (Table 7.2).

7.3.3 Field experiments

Two 'colonization-type' field experiments tested if secondary production varied among *Cystophora* species, epiphyte species, seasons and reefs. These experiments were carried out in tide pools or shallow tidal channels at Kaikoura. For each experiment, ca 15 cm lengths of distal fronds of each *Cystophora* species without epiphytes were collected. Fronds were transported to the laboratory where they were defaunated by shaking and rinsing with seawater. Examination showed that this method removed > 95% of mobile invertebrates (Siciliano, unpubl. data). Epiphytes were collected from the same sites and defaunated before being added (see below) to the distal segment of the host species with cotton twine. Host species were attached using cable ties to 1-m long heavy chains (all fronds where separated from each other by > 50 cm). A Pendant Hobo logger was attached to each chain, recording temperature at 20 minute intervals. Chains were haphazardly placed in ca 50 cm deep tide pools or channels. Experiments ran for 2 weeks after which samples were collected by cutting the twine and swiftly adding each seaweed to a sealed plastic bag for transport to the laboratory.

7.3.4 Experiment 1: effects of primary and secondary habitat formers

The first experiment tested if secondary production of invertebrates differed among three *Cystophora* species with and without epiphytes (*Jania* and *Polysiphonia*). This experiment was done at a single reef in Kaikoura (42°25'53.6"S, 173°41'27.7"E) and emulated the survey but controlled the abundance of the seaweeds and the initial invertebrate community (it was removed). The experimental design was: 3 *Cystophora* species × 3 epiphyte species (none, *Jania*, *Polysiphonia*) × 2 seasons × 4 replicates. The experiment was set up on 1st June and 13th December 2015.

7.3.5 Experiment 2: effects of secondary habitat former type and biomass

The second experiment tested if secondary production changed with epiphyte biomass, epiphyte type (i.e., a live epiphyte vs a non-living mimic) and between reefs using the

experimental design: 5 epiphytes levels/types (no epiphyte or low and high biomass of either living or mimic epiphytes) × 2 reefs (> 2 km apart, in Kaikoura) × 2 seasons × 4 replicates. *C. scalaris* and *Polysiphonia* were the primary and secondary habitat former species, respectively, because the survey showed that these species were inhabited by abundant invertebrates across study reefs and because *Polysiphonia* was morphologically distinct from *C. scalaris* (Appendix 3-6.2). *Polysiphonia* was added to *C. scalaris* at a high and low biomass (0.17 ± 0.02 vs 0.06 ± 0.02 gDW epiphyte/gDW host), where the high level corresponded to typical high levels found in the field survey. Similarly, high and low biomass of a non-living epiphyte mimic were added to *C. scalaris* hosts. These mimics were created from plastic fry-pan scrapers, that were cut, twisted and wrapped to provide a shape that was different from the host and that, at least superficially, mimicked *Polysiphonia* (Appendix 3-6.2). Adding mimics tested whether invertebrates colonized mainly live and edible habitat or if they also colonized non-living structures. The experiments were set up on 24th September and 13th December 2015.

7.3.6 Laboratory analysis

In the laboratory, samples were rinsed through a 250 µm and a 1-cm sieves to split organisms into small and large animals and to remove sediments and micro-organisms. Primary and secondary habitat formers were separated, identified and weighed after drying at 55°C for 48 h or until no further weight loss could be detected. Invertebrates were identified and counted as crustaceans (except caprellids), caprellids, molluscs, polychaetes, or 'other' invertebrates (based on Edgar's 1990b classifications) under a dissecting microscope at 40× magnification, and preserved in 70% ethanol (caprellids were separated from other crustaceans because they are distinct and easy to identify, and because Edgar reported a slightly different allometric model for these organisms). Finally, the average length of 600 small crustaceans and 600 small molluscs (representing > 94% of all counted invertebrates) was measured using a stereoscope and a reference scale (20 of each taxon, chosen randomly from 30 samples that represented different environmental and experimental conditions; Table 7.3).

7.3.7 Morphological traits of habitat formers

Morphological traits were quantified and compared between *Cystophora retroflexa*, *C. scalaris*, *C. torulosa*, *Jania*, *Polysiphonia* and *Polysiphonia* mimic. Measured traits included: surface area:dry weight ratios, fractal dimension, circularity (a measure of 'roundness', ranging from 0, for an infinitely elongated polygon, to 1, for a perfect circle, Sedgewick 2010) and lacunarity (Ferreira and Rasband 2012, an index of 'gappiness' or 'visual texture', considered a

measure of heterogeneity, Karperien 2007). Ten individuals of each species were blotted three times with paper towel and spread out on a white background to enhance the contrast for subsequent image analysis. For each sample a picture was taken with a Canon PowerShot G7X Mark II with ruler as a scaling reference. Each frond was then dried at 55°C for 48 h or until no further weight loss could be detected and its dry weight measured on a scale with three digits. Using Photoshop, each image was converted to grey scale and thresholded to binary images. Surface area:dry weight and circularity was calculated in ImageJ (Rasband 1997-2016), as was fractal dimensions and lacunarity, using the plugin FracLac (Karperien 1999-2013).

7.3.8 Calculations of secondary production and statistical analysis

To estimate the secondary production, invertebrate abundances were converted to biomass. 'Other' invertebrates were excluded from analyses because > 99.5% of counted organisms were in the four taxonomic groups with more precise published allometric relationships. For crustaceans and molluscs (respectively, 66.0% and 28.7% of all invertebrates) average length was used, whereas I assumed, for polychaetes and caprellids (respectively 4.6% and 0.4% of all invertebrates) that the average individual length was 625 μm (the mid-interval of a 250-1000 μm size range that include the vast majority of counted taxa; Siciliano, unpubl.). Finally, only 44 individuals were found to be large than 1 cm, and for these organisms I conservatively used 1 cm as their average sizes. The length of each organism was converted to biomass (mg AFDW) using taxon-specific length-weight relationships from Table 2 in Edgar (1990c) and summed across all individuals to estimate total faunal biomass per sample per taxonomic group. Faunal biomass per taxonomic group was then converted to production using the empirical equation $P = a \times B^b \times T^c$ (Edgar 1990c, page 200), where P is the daily production (mgC day^{-1}), B is the biomass (mg AFDW), and T is the water temperature (°C). For the survey, relevant medium summer temperatures were extracted from published figures from Cape Campbell, Kaikoura and Moeraki (2010 data from figure S3e, S4e and S5e in Schiel et al. 2016), and I assumed that temperatures at Pile Bay were in-between Kaikoura and Moeraki. For the experiments, mean temperature were calculated from the Pendant Hobo loggers. The coefficients a, b and c were derived for each taxonomic group from Table 5 in Edgar (1990c). Finally, carbon production was standardized per gram dry weight of the total seaweed biomass, that is, the combined weight of the primary and secondary habitat formers.

Effects of primary habitat former identity, secondary habitat formers identity and biomass, latitude and season were tested with permutation-based factorial analyses of variance based on Euclidean distances (PERMANOVA in the PRIMERv6/PERMANOVA+ software package; Clarke and Warwick 1994). In the second experiment, data from *Cystophora* species without epiphytes ('controls') were not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type (live vs mimic) and biomass (low vs high) (i.e., the controls were simply included to allow readers an opportunity to estimate magnitudes of facilitation cascades). Assumptions of normality and homogeneity of variances in the data sets were met. All factors were treated as fixed and 'Reef' was nested in 'Latitude'. Results were considered significant at $p \leq 0.05$ and were followed by post-hoc pair-wise t-tests (Anderson et al. 2008).

Trait data were square-root transformed, normalized and analyzed with multivariate permutation-based Anova (PERMANOVA), followed by post-hoc pair-wise t-tests, and visualized with Principal Coordinates Analysis (PCO).

7.4 RESULTS

7.4.1 Spatial survey: effects of primary and secondary habitat formers

A total of 177,269 invertebrates inhabited the seaweed fronds collected in the survey. Only two factors, 1st HF and Latitude, were significant and together accounted for 34% of the model variation (Table 7.1, $\eta^2 = SS_{Explained}/SS_{Total}$). Surprisingly, there was no effect of secondary habitat former or 2nd HF × 1st HF interaction. Invertebrate production was greatest (3.06 ± 0.23 mg AFDW day^{-1} gDW $Seaweed^{-1}$) at the northern reefs, intermediate at the two central locations, and least at southern reefs (1.24 ± 0.12) (pair-wise t-tests; Cape Campbell ≥ Pile Bay ≥ Kaikoura > Moeraki, Fig. 7.1A). The greatest invertebrate production was associated with *C. scalaris* (2.79 ± 0.18), intermediate for *C. retroflexa* (2.08 ± 0.19) and lowest associated with *C. torulosa* (1.39 ± 0.12) (based on pair-wise t-test; Fig. 7.1B), whether or not epiphytes were present. Invertebrate production was, as expected, dominated by production from crustaceans (70.2%), followed by molluscs (22.9%), polychaetes (6.7%) and caprellids (0.3%) (Fig. 7.1C-F).

7.4.2 Experiment 1: effects of primary and secondary habitat formers

A total of 51,794 invertebrates colonized the out-transplanted seaweeds in the first experiment. There was a significant 2nd HF × Season interaction ($p = 0.049$, $\eta^2 = 7.4\%$, Table 7.1),

highlighting greater invertebrate production with epiphytic *Polysiphonia* in winter but not in summer (t-test; Fig. 7.2A-B). 1st HF ($p = 0.017$) and Season ($p = 0.043$) were also significant as single factors, accounting for 12% and 5% of the data variability, respectively. Post-hoc t-tests showed that, averaged across treatments, *C. retroflexa* and *C. scalaris* supported similar secondary production (1.53 ± 0.67 mg AFDW day^{-1} gDW Seaweed^{-1}) which was significantly higher ($p < 0.05$) than *C. torulosa* (1.14 ± 0.10), and that production was greater in summer (1.52 ± 0.09) than winter (1.26 ± 0.13). Invertebrate production was, as in the survey, dominated by crustacean production (60.0%), followed by molluscs (36.2%), polychaetes (3.4%) and caprellids (0.3%) (Fig. 7.2C-F).

7.4.3 Experiment 2: effects of secondary habitat former type and biomass

In the second experiment, 110,608 invertebrates colonized the out-transplanted seaweeds.

There were three significant interactions, including a complex 3-way 2nd HF Type × Reef × Season interaction, explaining 6.4% of the data variability (Table 7.1). The most important interaction, however, was 2nd HF Type × Reef ($p = 0.001$, $\eta^2 = 18\%$), showing higher invertebrate production when the epiphyte was living compared to a mimic (Fig. 7.3A-B) but only in one of the two study reefs. The 2nd HF Type × 2nd HF Biomass interaction was also significant ($p > 0.01$, $\eta^2 = 5\%$), demonstrating that invertebrate production was greater when associated with live than mimic epiphytes and when living epiphytes occurred with large biomass (Fig. 7.3A-B). As expected, Season was the most important single factor ($\eta^2 = 32\%$), again showing higher invertebrate production in summer compared to winter (0.51 ± 0.09 mg AFDW day^{-1} gDW Seaweed^{-1} vs 0.40 ± 0.06, Fig. 7.3A-B). Finally, secondary production was dominated by crustaceans (62.9%) and molluscs (34.8%) and much less by polychaetes (1.7%) and caprellids (0.7%) (Fig. 7.3C-F).

7.4.4 Morphological traits of habitat formers

The PERMANOVA was highly significant ($p = 0.001$) and the t-tests showed significant differences between *C. retroflexa* and the two congeneric species, between living *Jania* and *Polysiphonia*, and between the artificial mimic and both epiphytes (see previous Chapter, 6.4.8, and Fig. 6.9-6.10).

7.5 DISCUSSION

Few studies have described facilitation cascades in a context of secondary production. Although the estimation of marine macroinvertebrate production is not new (see Buchanan and Warwick 1974, Collie 1985, George and Warwick 1985, Josefson 1982, Kristensen 1984, Vázquez and Rojas 1980, Warwick and Price 1975), only Valentine and Heck (1993) have quantified secondary production from co-existing habitat formers, reporting positive effects of mussels embedded in a seagrass bed. In addition, Pihl-Baden and Pihl (1984) suggested positive effects of the seaweed *Fucus vesiculosus* on invertebrate production within a seagrass bed but no data was shown for the productivity contribution from the seaweeds. Importantly, these studies measured production per area and did not take into account that biogenic biomass may be greater in the presence of a secondary habitat former. My study adds novel ecological insights by showing high secondary production of small invertebrates inhabiting marine primary producers, that morphologically similar-looking seaweeds can support different production levels, and that epiphytes, after taking biomass into account, did not increase secondary production.

7.5.1 Dominant taxa

Secondary production in both the survey and experiments was dominated by crustacean (except caprellids) and molluscs (accounting from 80-95% of all invertebrates) with very little production associated with caprellids and polychaetes. No other studies have compared production of these taxonomic groups associated with similar seaweeds but Taylor (1998a) and Cowles et al. (2009) showed that crustaceans and gastropods can dominate invertebrate production on canopy-forming seaweeds in New Zealand. Furthermore, although only few studies have quantified invertebrate production from seaweed habitats, many studies have shown that crustaceans and molluscs are the most numerous organisms on both canopy-forming seaweeds and seagrass around the world (Atalah and Crowe 2010, Battley et al. 2011, Cowles et al. 2009, Davenport et al. 1996, Gartner et al. 2013, Hooper and Davenport 2006, Taylor 1998a, Thomsen et al. 2016b). These results suggest that many processes (e.g., trophic transfer and carbon-cycling) in seaweed-dominated habitats, can be estimated from sampling crustaceans and molluscs, an insight of potential great value because exoskeletons and shells make these taxa more robust and suitable to experimental handling, long term preservation and taxonomic identification.

7.5.2 Primary habitat former identity

In contrast to my hypothesis, secondary production varied between the three congeneric *Cystophora* species, showing higher production associated with *C. scalaris* and *C. retroflexa* compared to *C. torulosa*. The greater production of the two species is probably explained by a slightly finer branched morphology compared to *C. torulosa* (Appendix 3-6.2) that may support greater invertebrate abundances. Although no other study has compared secondary production associated with different congeneric primary producers, other studies have compared production across habitats of different complexities. For example, Taylor (1998a) and Cowles et al. (2009) compared several intertidal and subtidal marine habitats (e.g., coralline turf, canopy-forming seaweed, seagrass, urchin barrens and mudflats), showing that the most 'complex' habitats were inhabited by more invertebrates and therefore had higher secondary production. These structurally finer types of habitats are likely, at least for very small invertebrates, to provide better shelter from predation and buffering of environmental stress (Coull and Wells 1983, Cowles et al. 2009, Edgar 1983, Heck and Thoman 1981, Taylor and Cole 1994).

7.5.3 Secondary habitat former presence and identity

There was no effect of epiphytes on secondary production in the survey or the first experiment even though *Cystophora* with epiphytes were clearly inhabited by more invertebrates (Table 7.2). This lack of effect was partly because invertebrate abundances differed only little between treatments but, more importantly, because production was standardized by the total biomass of habitat-forming species (i.e., the combined biomass of the primary and secondary habitat formers). I am not aware of other studies that have quantified effects of epiphytes on secondary production but several studies (none of which standardized data by total seaweed biomass) have reported positive effects of epiphytes on invertebrate abundances such as for the obligate epiphyte *Notheia anomala* on *Hormosira banksii* (Thomsen et al. 2016b) or for different mimics (Martin-Smith 1993) or live (Buzá-Jacobucci and Pereira-Leite 2014) epiphytes on various *Sargassum* host species. These positive effects have mainly been attributed to epiphytes providing additional and structurally more complex habitat compared to the host (Buzá-Jacobucci and Pereira-Leite 2014, Martin-Smith 1993, Thomsen et al. 2016b).

7.5.4 Secondary habitat former type and biomass

Despite the lack of effects of epiphytes in the first experiment, the second experiment did show higher production on *Cystophora* with high *Polysiphonia* biomass. This suggests that a

minimal epiphyte biomass can be required to trigger colonization and positive effects on secondary production. Similar positive density-dependency has been shown for abundances of animals associated with secondary habitat formers in seaweed beds (Buzá-Jacobucci and Pereira-Leite 2014, Thomsen et al. 2016b), seagrass beds (Hall and Bell 1988), forests (Bennetts et al. 1996), saltmarshes (Angelini et al. 2015) and mangroves (Bishop et al. 2012, Bishop et al. 2013, MacDonald et al. 2008). These studies therefore indicate that animal abundances correlates with greater habitat availability (Heck Jr and Orth 1980, Stoner and Lewis 1985) which provides additional space for settlement and colonization (Jacobi and Langevin 1996), a higher likelihood of finding different microhabitats (Buzá-Jacobucci and Pereira-Leite 2014) and different trophic resources (Bologna and Heck 1999). However, studies that compared invertebrates associated with living and artificial epiphytes have reported conflicting results. For example, Hall and Bell (1988) and Gartner et al. (2013) found comparable communities on living and artificial epiphytes of seagrass, concluding that structural effects are more important than trophic subsidies. By contrast, Bologna and Heck (1999, 2000), using artificial seagrass blades, found, like us, more invertebrates on living epiphytes compared to mimics, suggesting that trophic subsidies (or other traits associated with living structures) are important in controlling these invertebrate communities.

7.5.5 Latitudes and seasons

As expected, I found greatest and smallest secondary production at the northern and southern sample sites, respectively, in part because more invertebrates were found at the northern sites, in part because it was warmer there. Patterns were less clear for the two central latitudinal sites, characterized by minor temperature differences and slightly more invertebrates at Pile Bay compared to Kaikoura. There were also strong seasonal effects in the two experiments, with highest production in summer, where it was ca 3°C warmer. These results follow typical patterns from temperate systems with higher invertebrate abundances in warmer months (Arroyo et al. 2006, Rueda et al. 2008, Thomsen et al. 2016b, Wernberg et al. 2004). More specifically, Nakaoka (1989, 1992a, b) recorded peak spring growth of the bivalve *Yoldia notabilis*, and therefore also higher production, a season which contributed up to the 90% of total annual production (Nakaoka 1992b). Similarly, Donn and Croker (1986) demonstrated that the production of the amphipod *Haustorius canadensis* was greatest during summer. A few other marine benthic studies have also found greatest community-wide production in spring or summer, with data from subtidal rocky shore habitats (Taylor 1998a), intertidal salt marshes (Sarda et al. 1995) and intertidal lagoons (Sprung 1994). However, in contrast to these

consistent seasonal results, at least one study from New Zealand found no seasonal effects on abundances and production of invertebrates across different coastal habitats (Cowles et al. 2009).

7.5.6 Comparing secondary production and future studies

Here I standardized secondary production by the combined biomass of primary and secondary habitat formers, so that positive effects of epiphytes reflect that the epiphyte supports disproportionally more invertebrates than the host. This new biomass-standardization revealed few statistical effects of epiphytes on secondary production, suggesting that the host and epiphyte, in my system, provide relatively similar habitat quality on a gram-per-gram basis. By comparison, most studies that report secondary production of marine benthic invertebrates standardize data per area (Cardoso et al. 2004, Cowles et al. 2009, Fredette and Diaz 1990, Mistri et al. 2001, Nakaoka 1992b, Pihl-Baden and Pihl 1984, Taylor 1998a). To enable comparisons to these studies, I measured the typical dry weight of intertidal *C. torulosa* to be 839.30 gDW m^{-2} (± 102.09, n = 5, from 0.25×0.25 m quadrats collected from *Cystophora* beds near the experimental sites). Based on these data, my biomass-based abundances correspond to ca 230,000 ind. m^{-2} (and ca 1.72 g AFDW m^{-2}) inhabiting a typical *Cystophora* bed. These densities correspond to production rates of 1.55 g C^{-1} m^{-2} day^{-2} and are slightly greater than subtidal coralline turf, the canopy-forming seaweed *Carpophyllum plumosum* and *Ecklonia radiata* fronds and similar to the intertidal coralline turf (Cowles et al. 2009). I also argue that the method used here to estimate secondary production is a good first approximation to estimate community-wide invertebrate production, particularly where the local taxonomy is poorly described, organisms are small and inconspicuous, and where it is difficult to measure real production with repeated measurements such as through cohort analysis (Edgar 1990c). Nevertheless, over- or underestimation of production may arise, for example because the allometric regressions used here represent very coarse animal classifications or from fluctuation of food availability (from either food surplus and shortage, again, not considered here) (Edgar 1990c). Furthermore, in the regression models used here (Edgar 1990c), only temperature was included as an abiotic modifier and future studies should therefore test if other environmental conditions such as turbidity or wave exposure, further modify secondary production of small mobile invertebrates. Finally, I note that invertebrate losses, for example through predation or storms, was not quantified. Many other studies have shown that fish in particular can be strong consumers of small invertebrates (Martin-Smith 1993, Williams et al.

2002), and modify the strength of facilitation cascades (Adams et al. 2004, Edgar and Robertson 1992, Gribben et al. 2017b, Jaxion-Harm and Speight 2012). Clearly, more studies like these should test how opposing mechanisms like bottom-up habitat formation and top-down predation, in concert, control secondary production within and across habitats and ecosystems.

7.5.7 Conclusions

Facilitation cascades have been identified in many habitats and ecosystems as key processes that increases biodiversity in areal-based samples (Thomsen et al. 2018). I supplemented this rapidly expanding research topic by showing that (i) facilitation cascades can, in addition to modify animal community structures, affect secondary production, and, importantly, (ii) facilitation from the secondary habitat former can turn to neutral effects if production is converted from areal- to biomass-based estimates. I finally suggest that these new results are tested for consistency (or lack of) in many other habitats and ecosystems where facilitation cascades are ecologically important.

Tables

Table 7.1 Testing for effects of primary and secondary habitat formers on secondary production (mg AFDW day^{-1} Seaweed^{-1}) with Permutation-based factorial analysis of variance. All factors were treated as fixed and 'Reef' was nested in 'Latitude'. Univariate variables were analyzed with Euclidean distance. Note that invertebrate data was standardized per gram dry weight of seaweed (combined biomass of primary and secondary habitat formers). Significant values are in bold. Df = Degrees of freedom, SS = sum of squares, F = Pseudo-F, $\eta^2 = SS_{Explained}/SS_{Total}$.

Source	Df	SS	F	P	η^2
Spatial survey: effects of primary and secondary habitat formers					
2nd HF (2HF)	1	0.03	0.02	0.896	0.01
1st HF (1HF)	2	72.27	22.51	**0.001**	16.69
Latitude (Lat)	3	74.43	15.45	**0.001**	17.19
Reef(Latitude) Ree(Lat)	4	14.20	2.21	0.072	3.28
2HF × 1HF	2	4.54	1.41	0.219	1.05
2HF × Lat	3	6.11	1.27	0.305	1.41
1HF × Lat	6	7.40	0.77	0.585	1.71
2HF × Ree(Lat)	4	4.80	0.75	0.578	1.11
1HF × Ree(Lat)	6	6.70	0.70	0.627	1.55
2HF × 1HF × Lat	5	5.84	0.73	0.600	1.35
2HF × 1HF × Ree(Lat)	6	2.27	0.24	0.964	0.52
Res	146	234.41			
Total	188	433.00			
Experiment 1: effects of primary and secondary habitat formers					
2nd HF (2HF)	2	1.69	2.967	0.054	6.57
1st HF (1HF)	2	3.02	5.284	**0.017**	11.70
Season (Sea)	1	1.37	4.795	**0.043**	5.31
2HF × 1HF	4	0.69	0.605	0.670	2.68
2HF × Sea	2	1.89	3.320	**0.049**	7.35
1HF × Sea	2	1.78	3.112	0.052	6.89
2HF × 1HF × Sea	4	1.92	1.682	0.174	7.45
Res	47	13.41			
Total	64	25.77			
Experiment 2: effects of secondary habitat former type and biomass					
2nd HF biomass (Bio)	1	0.19	1.712	0.204	1.05
2nd HF type (Typ)	1	1.12	9.803	**0.006**	6.02
Reef (Ree)	1	0.78	6.888	**0.013**	4.23
Season (Sea)	1	5.90	51.815	**0.001**	31.81
Bio × Typ	1	0.94	8.239	**0.007**	5.06
Bio × Ree	1	0.10	0.834	0.380	0.51
Bio × Sea	1	0.01	0.085	0.778	0.05
Typ × Ree	1	3.31	29.085	**0.001**	17.85

Typ × Sea	1	0.00	0.027	0.868	0.02
Ree × Sea	1	0.00	0.026	0.892	0.02
Bio × Typ × Ree	1	0.00	0.005	0.957	0.00
Bio × Typ × Sea	1	0.09	0.785	0.360	0.48
Bio × Ree × Sea	1	0.02	0.180	0.693	0.11
Typ × Ree × Sea	1	1.19	10.409	**0.003**	6.39
Bio × Typ × Ree × Sea	1	0.00	0.008	0.932	0.00
Res	43	4.90			
Total	58	18.55			

Table 7.2 Biomass of primary and secondary habitat formers (1st and 2nd HF, in gram dry weight) and abundances of seaweed-associated invertebrates used to calculate invertebrate production per unit seaweed biomass. R = *Cystophora retroflexa*, S = *C. scalaris*, T = *C. torulosa*, E = Epiphyte (dominated by *Jania micrarthrodia* and *Polysiphonia decipiens*), P = epiphytic *Polysiphonia*, J = epiphytic *Jania*, 1 = low epiphytic biomass, 2 = high epiphytic biomass, M = mimic of epiphytic *Polysiphonia*. n = 1 for treatment RP for Exp1 7.3A - Summer (i.e., 2 replicates were unfortunately lost).

	Figure	Treatment	gDW 1HF			gDW 2nd HF			Invertebrates Abundance		
Survey	7.2A	Cape Campbell	2.725	±	0.225	0.385	±	0.125	963.833	±	93.847
		Kaikoura	4.699	±	0.916	0.950	±	0.339	1052.940	±	201.392
		Pile Bay	2.465	±	0.173	0.326	±	0.095	875.318	±	117.484
		Moeraki	4.302	±	0.335	1.947	±	0.384	884.302	±	85.419
	7.2B-C-D-E-F	R	2.777	±	0.472	0.000	±	0.000	762.500	±	137.376
		S	3.067	±	0.396	0.000	±	0.000	705.483	±	80.273
		T	3.168	±	0.293	0.000	±	0.000	318.808	±	32.844
		RE	3.912	±	0.669	2.417	±	0.593	1120.176	±	208.016
		SE	3.079	±	0.320	1.181	±	0.246	1173.085	±	96.210
		TE	5.702	±	1.170	1.956	±	0.539	1242.556	±	258.655
Exp1	7.3A Summer	R	1.985	±	0.448	0.000	±	0.000	614.750	±	158.486
		S	3.755	±	0.631	0.000	±	0.000	1006.500	±	179.883
		T	3.780	±	0.627	0.000	±	0.000	484.250	±	98.807
		RJ	1.925	±	0.709	2.181	±	0.310	1516.250	±	211.171
		SJ	4.072	±	0.702	3.610	±	0.564	2070.000	±	459.595
		TJ	3.045	±	0.257	2.275	±	0.234	1319.500	±	208.072
		RP	2.330			0.150			1254.000		
		SP	4.594	±	0.683	0.397	±	0.192	1242.000	±	183.780
		TP	4.432	±	1.019	0.156	±	0.023	1040.000	±	283.812
	7.3B Winter	R	1.292	±	0.333	0.000	±	0.000	188.500	±	76.612
		S	2.425	±	0.459	0.000	±	0.000	355.500	±	38.124
		T	2.162	±	0.330	0.000	±	0.000	292.000	±	55.955
		RJ	0.468	±	0.081	1.078	±	0.253	279.750	±	67.883
		SJ	1.334	±	0.297	1.586	±	0.764	481.667	±	159.642
		TJ	2.441	±	0.319	2.520	±	0.564	709.500	±	136.421
		RP	1.301	±	0.301	0.170	±	0.071	449.333	±	221.557
		SP	1.183	±	0.276	0.384	±	0.054	635.667	±	94.981
		TP	2.920	±	0.778	0.352	±	0.096	670.250	±	98.148
	7.3C-D-E-F	R	1.639	±	0.290	0.000	±	0.000	401.625	±	114.582
		S	3.090	±	0.440	0.000	±	0.000	681.000	±	149.603
		T	2.971	±	0.448	0.000	±	0.000	388.125	±	63.898
		RJ	1.196	±	0.430	1.630	±	0.279	898.000	±	255.241
		SJ	2.899	±	0.678	2.743	±	0.584	1389.286	±	408.611
		TJ	2.743	±	0.221	2.397	±	0.287	1014.500	±	162.956
		RP	1.559	±	0.334	0.165	±	0.050	650.500	±	254.974
		SP	2.889	±	0.831	0.390	±	0.089	938.833	±	164.138
		TP	3.676	±	0.659	0.254	±	0.055	855.125	±	155.587

Exp2	7.4A	S	3.690	±	0.356	0.000	±	0.000	926.000	±	120.401
	Summer	SM1	3.489	±	0.389	1.715	±	0.148	1363.375	±	191.903
		SM2	4.315	±	0.580	3.540	±	0.140	1949.125	±	226.365
		SP1	4.266	±	0.482	0.312	±	0.175	1218.200	±	118.688
		SP2	4.746	±	0.677	0.636	±	0.168	1793.500	±	324.264
	7.4B	S	7.264	±	1.007	0.004	±	0.004	933.750	±	126.784
	Winter	SM1	6.625	±	0.735	1.714	±	0.165	1525.125	±	320.365
		SM2	7.787	±	0.776	4.124	±	0.333	2018.375	±	331.277
		SP1	4.835	±	0.485	0.192	±	0.048	826.500	±	87.543
		SP2	6.524	±	0.740	1.152	±	0.151	2304.000	±	217.926
	7.4C-D-E-F	S	5.596	±	0.722	0.002	±	0.002	930.133	±	84.775
		SM1	5.057	±	0.570	1.714	±	0.107	1444.250	±	181.595
		SM2	6.051	±	0.648	3.832	±	0.190	1983.750	±	194.018
		SP1	4.616	±	0.347	0.238	±	0.071	977.154	±	87.082
		SP2	5.762	±	0.551	0.931	±	0.129	2085.214	±	191.975

Table 7.3 Average lengths (in mm, ± SE) for the most common taxa (crustaceans and molluscs). A total of 600 crustaceans and 600 molluscs were measured. n = number of individuals measured per sample (N). Each individual was measured under a stereoscope at 40× magnification using a high precision reference scale.

	N	Crustaceans (mm)	*n*	Molluscs (mm)	*n*
Survey	16	1.748 ± 0.078	20	1.330 ± 0.124	20
Experiment 1	6	1.540 ± 0.057	20	1.135 ± 0.047	20
Experiment 2	8	1.566 ± 0.092	20	1.340 ± 0.098	20

Figures

Figure 7.1 Spatial survey, effects of primary and secondary habitat formers. Secondary production (mg AFDW day^{-1} Seaweed^{-1}) per latitude (A) and per primary habitat former (1HF, *Cystophora retroflexa*, *C. scalaris*, *C. torulosa*) with and without epiphytes (2nd HF, dominated by *Jania micrarthrodia* and *Polysiphonia decipiens*) (B-F). Data were standardized by dry weight of primary and secondary habitat formers (1st + 2nd HF). Error bars = 1 SE, n = 32 for A (the test factors '1st HF', '2nd HF' and 'Reef' were pooled), n = 48 for B-F (the test factor 'Latitude' and 'Reef' were pooled). Different letters indicate significant differences as detected by pair-wise t-test comparisons.

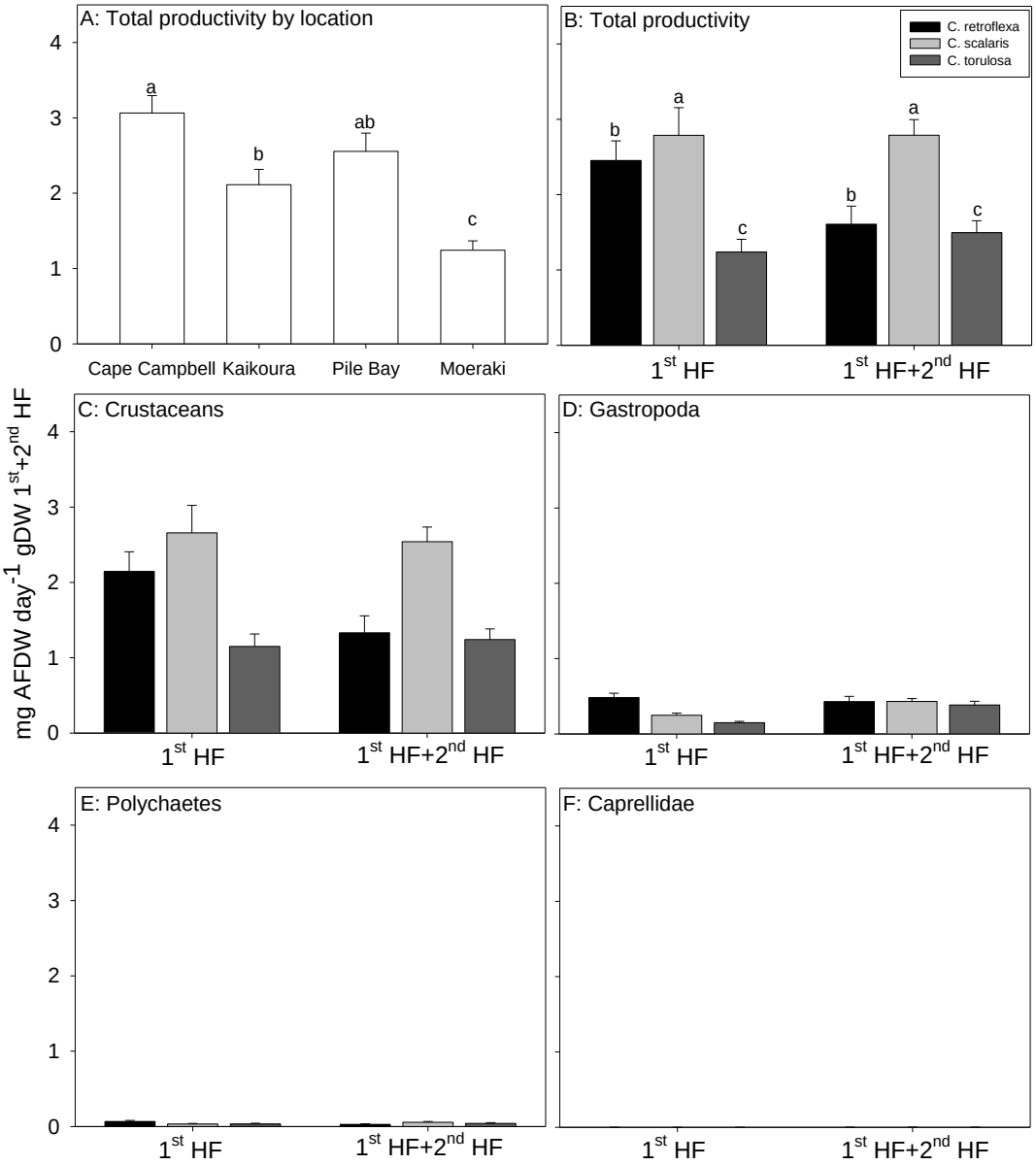


Figure 7.2 Experiment 1, effects of primary and secondary habitat formers. Secondary production (mg AFDW day^{-1} Seaweed^{-1}) per primary habitat former (1HF, *Cystophora retroflexa*, *C. scalaris*, *C. torulosa*) with and without epiphytes (J = *Jania micrarthrodia*, P = *Polysiphonia decipiens*) in summer (A) and winter (B). Data were standardized by dry weight of the total association of primary and secondary habitat formers (1st + 2nd HF). Error bars = 1 SE, n = 4 for A-B and n = 8 for C-F. There are no error bars for samples with no replicates. Capital letters refers to the 'season' test factor, lower case letters to the 'primary habitat former' factor.

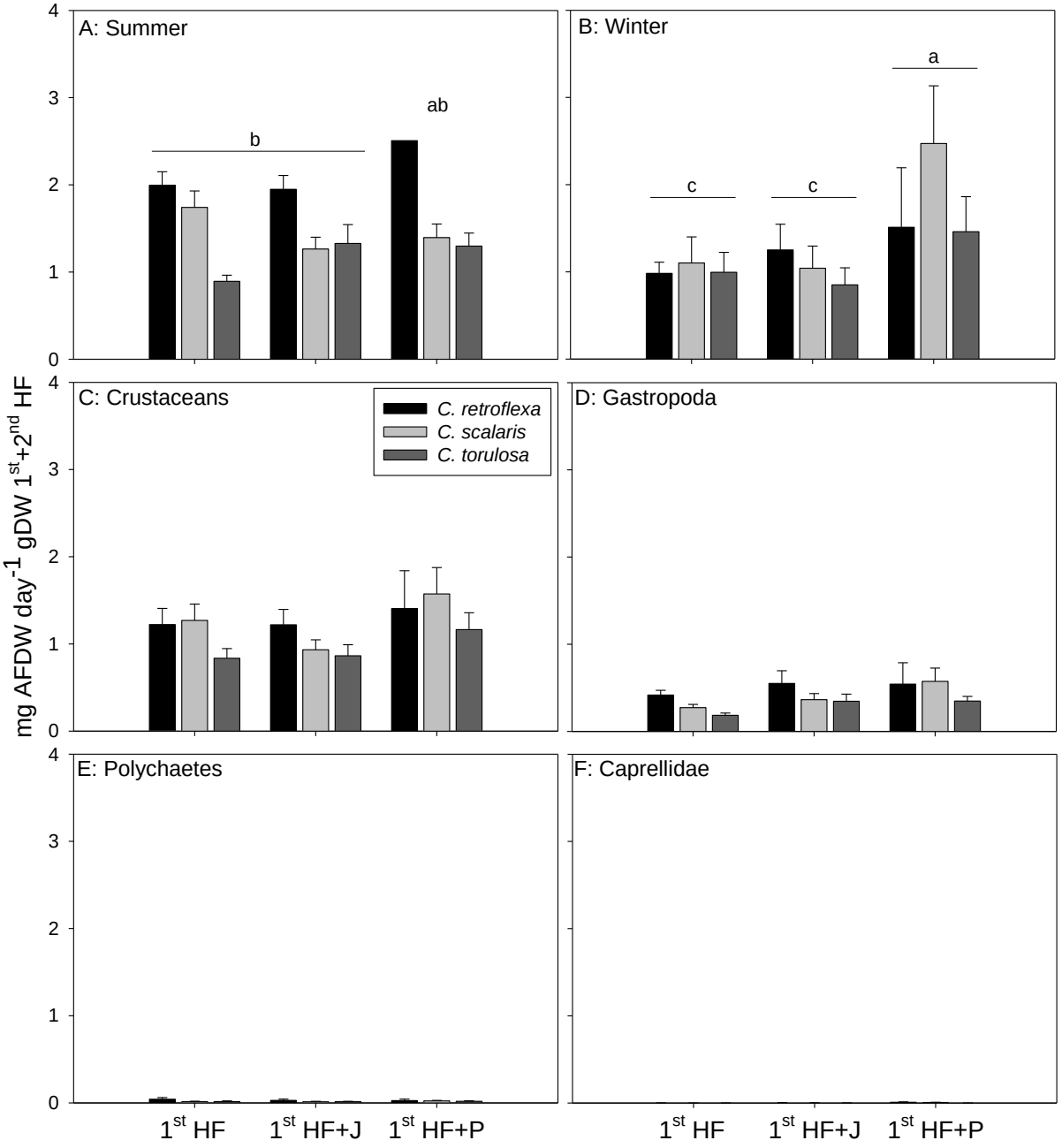
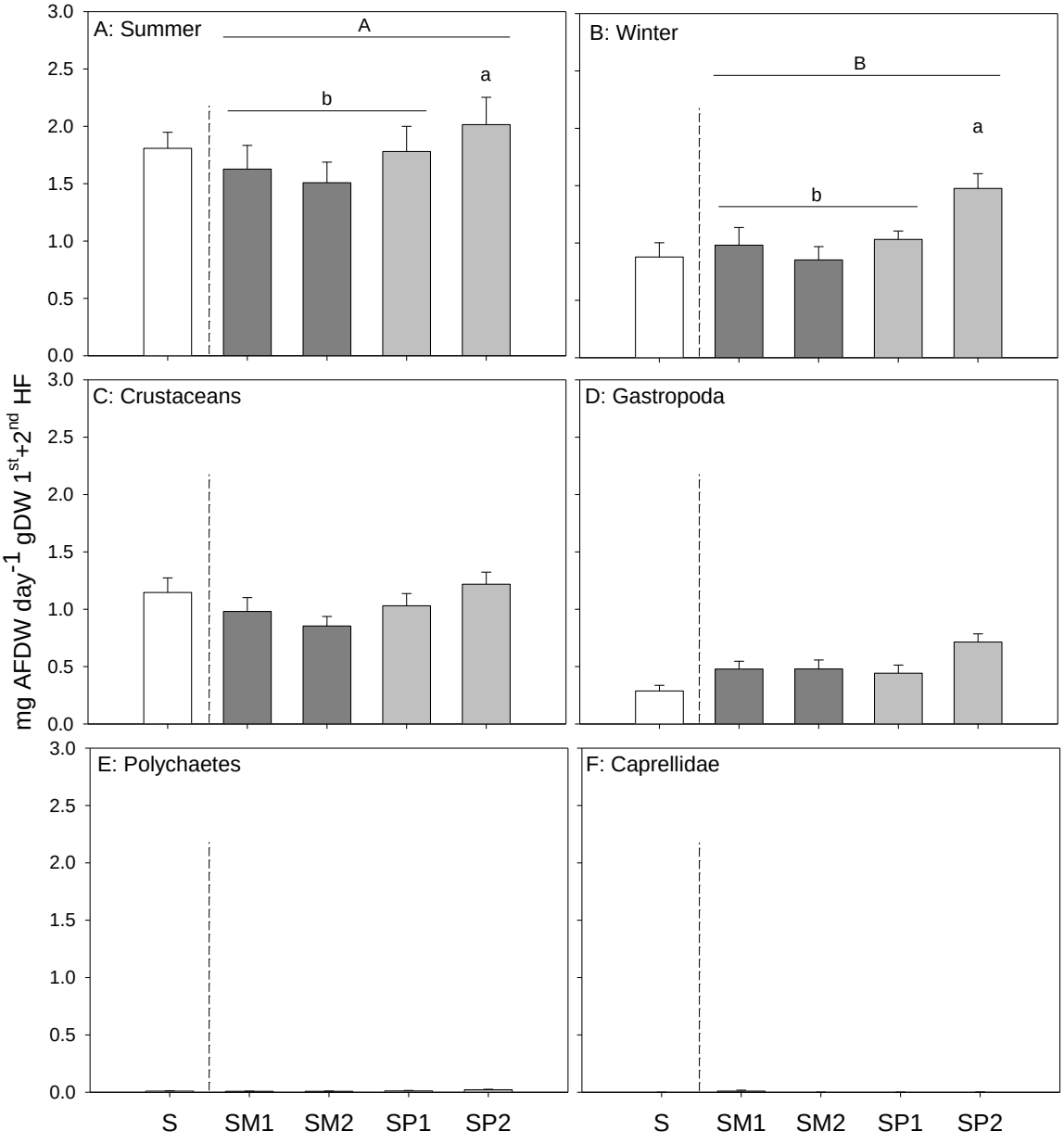


Figure 7.3 Experiment 2, effects of secondary habitat former type and biomass. Secondary production (mg AFDW day^{-1} Seaweed^{-1}) associated with *Cystophora scalaris* (S) with and without epiphytic *Polysiphonia decipiens* (P) and a *Polysiphonia* mimic (M) in both low (1) and high (2) biomasses, in summer (A) and winter (B). Data were standardized by dry weight of the total association of primary and secondary habitat formers (1st + 2nd HF). The control treatment without epiphytes (S, n = 4) was not included in the statistical analysis because the objective here was testing for interaction effects between secondary habitat former type and biomass. Error bars = 1 SE, n = 4 for A-B and n = 8 for C-F. Capital letters refers to the 'season' test factor, lower case letters to the '2nd HF Type × 2nd HF Biomass' interaction.



CHAPTER 8: General discussion

In this thesis, I investigated facilitation and habitat cascades associated with ecologically and morphologically different co-occurring habitat-forming species, including bivalves, seagrass and canopy-forming and epiphytic seaweeds. More specifically, I assessed the role of these co-occurring habitat formers in affecting invertebrate communities in intertidal soft-bottom estuarine shell beds, seagrass beds and on rocky shores. I tested which natural or anthropogenic environmental factors increased, decreased or altered the effects of these interactions and I correlated morphological traits of the habitat formers with invertebrate abundances, taxonomic richness and community structures (Chapter 2-6). I also examined how these habitat-forming species modify environmental parameters such as light intensity, temperature and water loss (Appendix 1). The main results of my observational surveys and manipulative experiments are summarized in Table 8.1, where the ecological importance of factors tested in each data chapter is evaluated. For simplicity, I focus on individual test factors here, excluding complex interaction effects that were discussed in more detail in the individual data chapters.

8.1 Variability within habitat: soft-bottom shell beds, seagrass beds and rocky shores

8.1.1 Soft-bottom shell beds. In the soft-bottom shell beds, bivalve-seaweed-invertebrate habitat cascades (Chapter 2) were mostly affected by large-scale spatial variability (but with no clear latitudinal patterns) and seasonality (summer > winter) across response variables. At the level of the secondary habitat former, the living/edible condition was the most relevant factor (living > artificial), followed by species identity (*Ulva* sp. > *Gracilaria chilensis*) and its biomass (low > high). The effects of small-scale spatial variability such as site (Site X ≠ Site Y) and elevation (subtidal > intertidal), and the condition of the primary habitat former (mimic > shell = alive), were of less importance but could nevertheless also modify the cascade. The critical role of the secondary habitat former was confirmed in my 'long' habitat cascade study (Chapter 3) where the presence of a secondary habitat former (presence > absence) and its biomass (high > low) were the most important factors. These two data chapters support previous evidence of habitat cascades based on two (Albrecht and Reise 1994, Thomsen et al. 2010) or multiple habitat-forming (Thomsen et al. 2016a, Yakovis and Artemieva 2017) species from bivalve-dominated soft-bottom estuaries. In addition, I also showed that living secondary habitat formers supported higher biodiversity than mimics whereas the type of the

primary habitat former was less relevant. This is probably due to the fact that seaweeds benefit from the bivalve only in terms of settlement space, regardless of its condition (i.e., living = dead = mimic) as most seaweeds can colonize and grow on a variety of hard substrates, including rocks, boulder, stones and living or dead shells (Baker 1912, Ben-Avkaham 1971, Lutaenko and Levenets 2015).

8.1.2 Seagrass beds. Invertebrate abundances and community structures were affected by all the factors tested in the soft-bottom seagrass beds (Chapter 4) whereas richness was either unaffected (in relation to season, site and secondary habitat former type) or only weakly affected (by estuary and elevation). In general, long temporal (Year 1 ≠ Year 2) and large spatial (North = Central > South) variability, as well as presence of primary (presence > absence) and secondary (presence > absence) habitat formers, strongly affected this seagrass-seaweed cascade. Furthermore, in the complementary chapter (Chapter 5), sedimentation (but not fertilization) modified the effects of all the factors tested, ultimately killing the seagrass and destroying the habitat cascade. My results support past studies that have documented positive effect of seaweeds (as epiphytes or drift algae) within seagrass beds, where facilitation has been attributed to reduced predation (Adams et al. 2004, Leber 1985) or increment of habitat heterogeneity (Cardoso et al. 2004, Edgar and Robertson 1992, Hall and Bell 1988, Lewis III and Stoner 1983, Martin-Smith 1993, Stoner and Lewis 1985). Although negative impacts of sedimentation on seagrasses have been reported in several studies (see Cabaço et al. 2008), none of these studies have examined impacts on seagrass-associated invertebrates or how entire habitat cascades can be destroyed.

8.1.3 Rocky shores. The seaweed-epiphyte-gastropods habitat cascade from the rocky shore (Chapter 6) was primarily affected by latitude (North > South), season (abundance: summer > winter; richness: winter > summer) and reef (Reef 1 ≠ Reef 2). All attributes of both the primary (species: *C. retroflexa* > *C. scalaris* > *C. torulosa*; biomass: high > low) and secondary habitat former (presence: presence > absence; species: *Polysiphonia* > *Jania*; type: living > artificial; biomass: high > low) affected abundance, richness and community structures of gastropods. This chapter confirms the relevant role of habitat cascades in rocky shores, previously demonstrated for both subtidal (Bell et al. 2014, Rohr et al. 2011) and intertidal (Thomsen et al. 2016b, Viejo and Åberg 2003) systems. Although not tested in detail here, my results provide indirect support for previously documented underpinning facilitation mechanisms, suggesting that primary and secondary habitat-forming seaweeds provide food (Bell et al. 2014,

Martin-Smith 1993, Rohr et al. 2011, Viejo and Åberg 2003), protection from predation (Bell et al. 2014, Rohr et al. 2011) and reduce stress (Viejo and Åberg 2003) for invertebrates. The second chapter from rocky shores (quantifying the impact on secondary production on entire invertebrate communities, Chapter 7) confirmed the important role of latitude (North > South) and season (summer > winter) but found no effect of the secondary habitat former. However, this discrepancy was largely explained by a different data standardization methodology, as invertebrate responses in Chapter 7 were standardized by seaweed biomass, instead of per seaweed sample (because the aim here was evaluating if epiphytes, compared to hosts, are hotspots of productivity). Indeed, if data were reported, as in traditional studies, without being standardized per seaweed biomass, secondary production increased dramatically in the presence of secondary habitat-forming epiphytes. This chapter thereby supports Valentine and Heck (1993), the only study reporting secondary productivity in habitat cascades, who found that mussels embedded in seagrass beds, also increased secondary production.

8.2 Variability across habitats: soft-bottom shell beds vs seagrass beds vs rocky shores

To date, only Thomsen et al. (2018, 2010) have compared habitat cascades among different ecosystems and habitats such as tropical, subtropical and temperate forests, seagrass beds and salt marshes. In this thesis I can compare cascades from three very different habitats, even if my primary focus was on the factors that affected a specific cascade. Indeed, these habitat cascades were measured with relatively similar procedures, i.e., using similar factorial design and spatio-temporal test factors. Across all the habitats investigated, spatial and temporal factors (latitude and season), as well as features of the secondary habitat former (presence, condition and biomass), were important factors affecting habitat cascades. The effect of local spatial variation (site and reef) was, instead, quite different between soft and hard-bottom habitats, appearing to be more important on the rocky shores.

8.3 Trophic vs structural benefits

Results from the experiments that compared living and non-living secondary habitat formers found relatively similar facilitation effects (Chapters 2-6). In the bivalve-seaweed cascade from soft-bottom estuaries, invertebrate abundances and richness were higher when the seaweed was living instead than when a mimic and the community structures differed strongly between the two seaweed types. In addition, the most important invertebrate taxa (trochid snails, amphipods

and copepods) all had strong preferences for living seaweeds. This is probably because these inhabitants typically are herbivores that, at least partly, consume their host. Many other studies have demonstrated that trochids, amphipods and copepods feed on seaweeds (Buzá-Jacobucci and Pereira-Leite 2014, Cruz-Rivera and Hay 2001, D'Antonio 1985, Grahame 1973, Hagerman 1966, Kamermans et al. 2002, McBane and Croker 1983, Pederson and Capuzzo 1984, Poore 1994, Watson and Norton 1987). In the seagrass beds, invertebrate abundance was strongly affected by the different type of secondary habitat former whereas richness was not. Again, the living seaweed (*Ulva*) hosted higher abundances and a different community structure compared to the mimic. These results reflect that trochids were the most abundant herbivorous molluscs in this habitat, and their dominance and preference for *Ulva* (over *Gracilaria* or mimics) had a strong effect on abundances but very little effect on richness (as *Gracilaria* and mimics typically also were inhabited by at least 1 trochid snail). Several studies demonstrated that seaweeds can represent important trophic resources for herbivorous invertebrates in seagrass beds (Bologna and Heck 1999, Boström and Mattila 1999, Byers et al. 2012, Gartner et al. 2013, Hall and Bell 1988, Kitting et al. 1984, Orth and Van Montfrans 1984, van Montfrans et al. 1984) and it has already been suggested that *Micrelenchus tenebrosus*, one of the most abundant trochids found here, grazes on *Ulva* (Thomsen et al. 2016a). Finally, on rocky shores, invertebrate abundances were less affected by the secondary habitat former condition, although living seaweeds still had higher richness and different community structures compared to mimics. This suggests that the majority of common invertebrates, in this system, inhabit structures to avoid predation rather than as a trophic resource (because mimics are not edible). Still, some of the less common invertebrates may still be facilitated by trophic resources explaining why richness (but not abundances) was higher on living seaweeds. On rocky shores, only one study has used artificial mimics, also concluding that mimics and living epiphytes provide comparable habitats (Martin-Smith 1993).

In concert, my results suggest that living habitat formers are more efficient than mimics in hosting invertebrates and that the majority of herbivorous taxa had a preference for living seaweeds rather than the mimics, as living seaweed can be an important food source (Bologna and Heck 1999, Boström and Mattila 1999, Byers et al. 2012, Gartner et al. 2013, Hall and Bell 1988, Kitting et al. 1984, Orth and Van Montfrans 1984, van Montfrans et al. 1984). Nevertheless, mimics functioned to some extent as living habitat formers, especially in the habitat without alternative tridimensional structures, as demonstrated in Chapter 4, where mimics had a strong positive effect on unvegetated mudflats.

8.4 Magnification ratios across habitat cascades and habitat formers

Thomsen et al. (2010) proposed to compare habitat cascades across systems and habitats using the 'magnification ratio' (MR), calculated as the ratio of the abundance (or richness) of the co-occurring primary and secondary habitat formers compared to the primary habitat former alone (MR = (1^{st} HF + 2^{nd} HF) / 1^{st} HF), where values > 1 correspond to a net positive effect of the secondary habitat former (i.e., to habitat cascades). Here, I calculated magnification ratios for the habitat cascades investigated in Chapters 2, 4, and 6. Importantly, MR depends on how facilitation of invertebrates is standardised (e.g., unstandardized, per sample area or biomass of habitat formers). Here I calculated all MR values as the number of invertebrates (or taxa) without any standardization, enabling easy and direct comparisons across habitat formers and habitats. I found highest MR values for the bivalve-seaweed cascade (Chapter 2, Fig. 8.1, abundance: 26-120, richness: 7-16), because few mobile invertebrates inhabited the shell surface (Gribben et al. 2009, Thomsen et al. 2016a). Magnification ratios for the seagrass-seaweed (Chapters 4-5) and seaweed-seaweed (Chapters 6-7) cascades ranged, instead, from 1-4 for abundances and 1-1.5 for richness (Fig. 8.1). Notably, all MR values, but two, were positive, ***providing strong support for my initial core hypothesis: habitat cascades are common processes in benthic intertidal systems***. Indeed, the only MR values below 1 were for the cascades *Zostera*-tape (*Ulva* mimic; abundance) and *Zostera*-*Ulva* (richness) in a single experiment. My results supported past data (Thomsen et al. 2010), as I found highest MR values when the secondary habitat former was functionally very different from the primary habitat former (more specifically, the secondary seaweed was form-functionally very different from the primary bivalve). I also found evidence of some habitat cascades when the secondary habitat former was an artificial mimic, with values comparable (and sometimes even higher) to relatively similar natural habitat formers. This result again supports the notion that biogenic habitat provides important structural support for invertebrates, and provides evidence that invertebrate colonization of artificial substrates is a common process in both seagrass beds (Barber et al. 1979, Bell et al. 1985, Schneider and Mann 1991b, Virnstein and Curran 1986) and rocky shores (Martin-Smith 1993). Note that the MR results described here (i.e., mimics provide benefits for inhabitants comparable to living habitat formers) contrast my conclusion from the previous section (8.3, stronger effect of living habitat formers over mimics). This discrepancy simply reflects the different standardization methods (no standardization vs per gram dry weight of the habitat-forming species).

8.5 Morphological comparisons between habitat formers

Structurally complex habitats often support more abundant and diverse animal communities compared to structurally simple habitats (Hauser et al. 2006), as shown for coral reefs (Almany 2004), forest canopies (MacArthur and MacArthur 1961), freshwater vegetation (Diehl 1992), soft-bottom marine systems (Talman et al. 2004), and algal communities (Choat and Kingett 1982, Hicks 1985). High habitat complexity increases the number of niches available for colonization (Hicks 1985), provides shelter and protection from physical stress (Gibbons 1988), increases food availability for invertebrates living on the algae (Hicks 1985) and can alter effects from competition and predation (Coull and Wells 1983, Diehl 1992, Hixon and Menge 1991). For example, complex habitat may reduce dislodgement from waves and currents (Gibbons 1988) and facilitate early settlement of larvae (Hauser et al. 2006). The habitat structure concept was discussed in detail by McCoy and Bell (1991), who argued that habitat structure encompasses both elements of 'complexity' and 'heterogeneity', where both habitat-effects and measurement are strongly scale-dependent (Beck 1998, Downes et al. 1998). Here complexity describes variation in abundances of distinct physical elements of the habitat such as rocks, crevices, holes, pits, and pneumatophores (Downes et al. 1998, McCoy and Bell 1991) whereas heterogeneity focusses more on the variation in the relative abundance of the different physical elements (Beck 1998, Downes et al. 1998, McCoy and Bell 1991).

In this thesis, I measured surface area:dry weight ratios (Hauser et al. 2006) and fractal complexity (Beck 1998, 2000, Gee and Warwick 1994a, Gee and Warwick 1994b) as measures of complexity, and lacunarity (Cúrdia et al. 2015) and circularity (Turon and Becerro 1992) as measures of heterogeneity. Based on these parameters, I compared the morphologies of the different studied habitat formers (Fig. 8.2) and discussed these morphological attributes in relation to abundances and richness of invertebrates found in habitat cascades. Here I compiled the morphological data from Chapters 2, 4 and 6, and arranged data from the highest to the lowest values (separately for living and artificial habitat formers). A multivariate PCO analysis (Fig. 8.2A) showed that the rocky shores species were clustered (*Cystophora* spp., *Hormosira*, *Jania*, *Polysiphonia*, *Notheia*), with more complex and similar fractal dimension and lacunarity, compared to the estuarine species (*Austrovenus*, *Ulva*, *Gracilaria*, *Zostera*) and their mimics. Morphological traits suggest that species that retain a large amount of water in their tissues such as *Ulva*, *Zostera* and *Gracilaria*, had higher surface area:dry weight ratios compared to the large fucoids (*Cystophora* species) and, in particular, the artificial (plastic) habitat formers. There were fewer differences in fractal dimensions among the habitat formers,

although *Hormosira*, *Zostera* and *Gracilaria* had relatively low values. Lacunarity was high for branched species such as *Gracilaria*, *Polysiphonia*, *Notheia*, *Jania*, and low for species lacking gaps such as *Ulva*, *Austrovenus* and *Zostera*. By contrast, circularity was highest for the bivalve *Austrovenus* and its mimic compared to habitat-forming primary producers. Importantly, in some cases (surface area:dry weight ratio and circularity) the artificial mimics showed similar patterns to living habitat formers (Fig. 8.2B, *Ulva* > *Gracilaria* > *Polysiphonia* > *Austrovenus*; Fig. 8.2D, *Austrovenus* > *Ulva* > *Polysiphonia* > *Gracilaria*), suggesting that the mimics mirrored some of the key morphological attributes.

Comparing invertebrate abundance and richness for the individual habitat formers (data from Chapter 2, 4, 6) my results suggest that:

- invertebrate abundance and richness was higher on *Ulva* than *Gracilaria*, and very few invertebrates were found on *Austrovenus* (Chapter 2; Fig. 2.1, spatial survey, Fig. 2.3, seasonal survey, Fig. 2.7A-C, experiment 2);
- invertebrate abundance and richness were higher on *Ulva* than *Zostera* (Chapter 4; Fig. 4.3, seasonal survey) and richness was higher on *Ulva* mimics than on *Gracilaria* mimics (Chapter 4; Fig. 4.7, experiment 2);
- gastropod abundance and richness decreased following this order of habitat formers: *C. retroflexa*, *C. scalaris*, *C. torulosa* and *H. banksii* (Chapter 6; Fig. 6.1, survey, Fig. 6.2, experiment 1).

These results are supported by the morphological analysis. The fractal dimension can explain the stronger effect of *Ulva* in hosting invertebrates compared to *Gracilaria* (and relative mimics, Chapter 2) and *Zostera* (Chapter 4) and, similarly, the stronger effects of *Cystophora* spp. compared to *Hormosira.* These results support past studies that have correlated fractal dimension to invertebrate data (Gee and Warwick 1994a, Gee and Warwick 1994b, Gunnarsson 1992, Hooper and Davenport 2006, Morse et al. 1985, Shorrocks et al. 1991, Tokeshi and Arakaki 2012). Additionally, lacunarity may explain the sequence of *Cystophora* spp. in hosting invertebrates (as there were no significant differences in fractal dimension) and why *Ulva* was inhabited by more invertebrates than *Zostera*. Lacunarity has not been studied much, but Cùrdia et al. (2015) found a positive correlation between lacunarity and taxonomic richness of invertebrates inhabiting the soft coral *Leptogorgia lusitanica* The surface area:dry weight ratio data also supports my results, showing higher values for *Ulva* over *Zostera* and *Gracilaria* and following the *Cystophora* spp. sequence. However, this parameter may not always be a useful predictor of invertebrate diversity (Hauser et al. 2006). Finally, circularity appeared to be a poor predictor of invertebrate biodiversity. I am not aware of any studies that

have quantified circularity of seaweeds or related circularity to habitat formation, but circularity has been calculated for sponges in the context of their competitive abilities (Becerro et al. 1994, Turon and Becerro 1992). Note that I did not discuss *Polysiphonia*, *Jania* and *Notheia* simply because these epiphytes were always collected with their host. It has been suggested habitat complexity generally should be explained based on multiple indices (Beck 2000) because a single morphological parameter is unlikely to encapsulate how different species respond to biogenic habitats (Hauser et al. 2006). My results suggest that surface:dry weight ratio, fractal dimension and lacunarity provide an important mixture of morphological attributes to explain how inhabitants utilize biogenic structures, and that these attributes therefore should be included in future models aiming to predict the strength of habitat cascades.

8.6 Suggestions for future research

I suggest that useful approaches to be implemented in future research for a better understanding of the dynamic of habitat cascades may include: (i) inferencing the effect of habitat cascades at a landscape level, (ii) investigating the individual effect of each single habitat former involved in the cascade and testing for complementarity and redundancy effects among habitat formers, (iii) implementing of multiple biodiverisity indices, (iv) comparative studies based on the estimation of secondary production in multiple ecosystems, (v) standardization of data based on the actual surface available to inhabitants.

8.7 Conclusions

My research has demonstrated that habitat cascades are important in controlling, maintaining and increasing biodiversity in marine benthic ecosystems where epibiosis is prevalent. In particular, habitat cascades are common processes in intertidal habitats and are geographically widespread and temporally and seasonally persistent. Intertidal habitats are harsh environments that affect invertebrates, seaweeds and seagrasses, ranging from species specific physiological stress to high predation levels and strong competition for limited space. Habitat cascades function by reducing these stressful environmental conditions and promoting ecosystem functions. My results also suggest that the strength of habitat cascades can be predicted based on (i) the ecological and morphological attributes of individual habitat formers in the cascade, (ii) how co-occurring habitat formers affect each other, (iii) the affinity of inhabitants for individual habitat formers, and (iv) the effects of anthropogenic stressors on the habitat

formers. These predictions should, in the future, be tested for generality in more ecosystems, and incorporated into models of species interactions.

Tables

Table 8.1 Overview of effects from individual test factors for habitat cascades from three different study systems. The effects of each factor are reported for invertebrate abundance (N), taxonomic richness (R), community structure (CS) and secondary production (P). -: factor not included in the design; 0: no effect of the factor; *, **, ***: significant effect levels. Lat = Latitude, Est = Estuary, Sea = Season, Hab = Habitat, Ele = Elevation, HF = habitat former (1, 2, 3HF = primary, secondary, tertiary HF, respectively), pre = Presence, sp = Species, bio = Biomass, Fe = Fertilization, Se = Sedimentation.

Habitat	Habitat cascade	Var	Factors																
			Year	Lat	Est	Sea	Hab	Site Reef	Ele	1HF pre	1HF sp	1HF type	2HF pre	2HF sp	2HF type	2HF bio	3HF pre	Fe	Se
Soft-bottom estuary	Ch. 2: Bivalve Seaweed Invertebrates	N	-	0	***	***	-	0	**	-	-	0	-	***	***	*	-	-	-
		R	-	**	***	***	-	*	**	-	-	**	-	**	***	**	-	-	-
		CS	-	***	***	***	-	**	***	-	-	0	-	**	***	***	-	-	-
	Ch. 3: Bivalve Seaweed Seaweed Invertebrates	N	-	-	**	0	0	0	0	-	-	-	-	-	-	***	***	-	-
		R	-	-	*	**	*	*	0	-	-	-	-	-	-	**	0	-	-
		CS	-	-	*	*	*	**	0	-	-	-	-	-	-	***	***	-	-
Seagrass soft-bottom system	Ch. 4: Seagrass Seaweed Invertebrates	N	***	***	***	***	-	**	***	***	-	***	***	-	***	***	-	-	-
		R	***	***	**	0	-	0	*	***	-	-	***	-	0	***	-	-	-
		CS	***	***	***	***	-	**	***	***	-	***	***	-	***	**	-	-	-
	Ch. 5: Seagrass Seaweed Invertebrates	N	-	-	-	**	-	0	0	0	-	-	0	-	-	-	-	0	***
		R	-	-	-	0	-	0	0	0	-	-	0	-	-	-	-	0	***
		CS	-	-	-	***	-	0	0	***	-	-	***	-	-	-	-	0	**

Rocky shore	Ch. 6: Seaweed Seaweed Gastropods	N	-	***	-	**	-	***	-	-	**	-	***	***	0	**	-	-	-
		R	-	***	-	***	-	**	-	-	*	-	0	**	**	**	-	-	-
		CS	-	***	-	***	-	***	-	-	**	-	***	***	**	**	-	-	-
	Ch. 7: Seaweed Seaweed Invertebrates	P	-	**	-	**	-	*		**	-	-	0	-	-	0	-	-	-

Figures

Figure 8.1 Magnification ratios relative to the abundance and richness of invertebrates for each main habitat cascade investigated in Chapters 2, 4, and 6, using living (grey) or artificial (dark grey) secondary habitat formers. A: *Austrovenus stutchburyi*, G: *Gracilaria chilensis*, U: *Ulva* sp., Z: *Zostera muelleri*, Ta: tape drifting seaweed mimic, Tw: twine drifting seaweed mimic, C: *Cystophora* spp., E: living epiphyte, H: *Hormosira banksii*, M: epiphyte mimic, S1: spatial survey, S2: seasonal survey, E1, Experiment 1, E2: experiment 2. Data used for the calculation have not been standardized. A value higher than 1 indicates the presence of a habitat cascade.

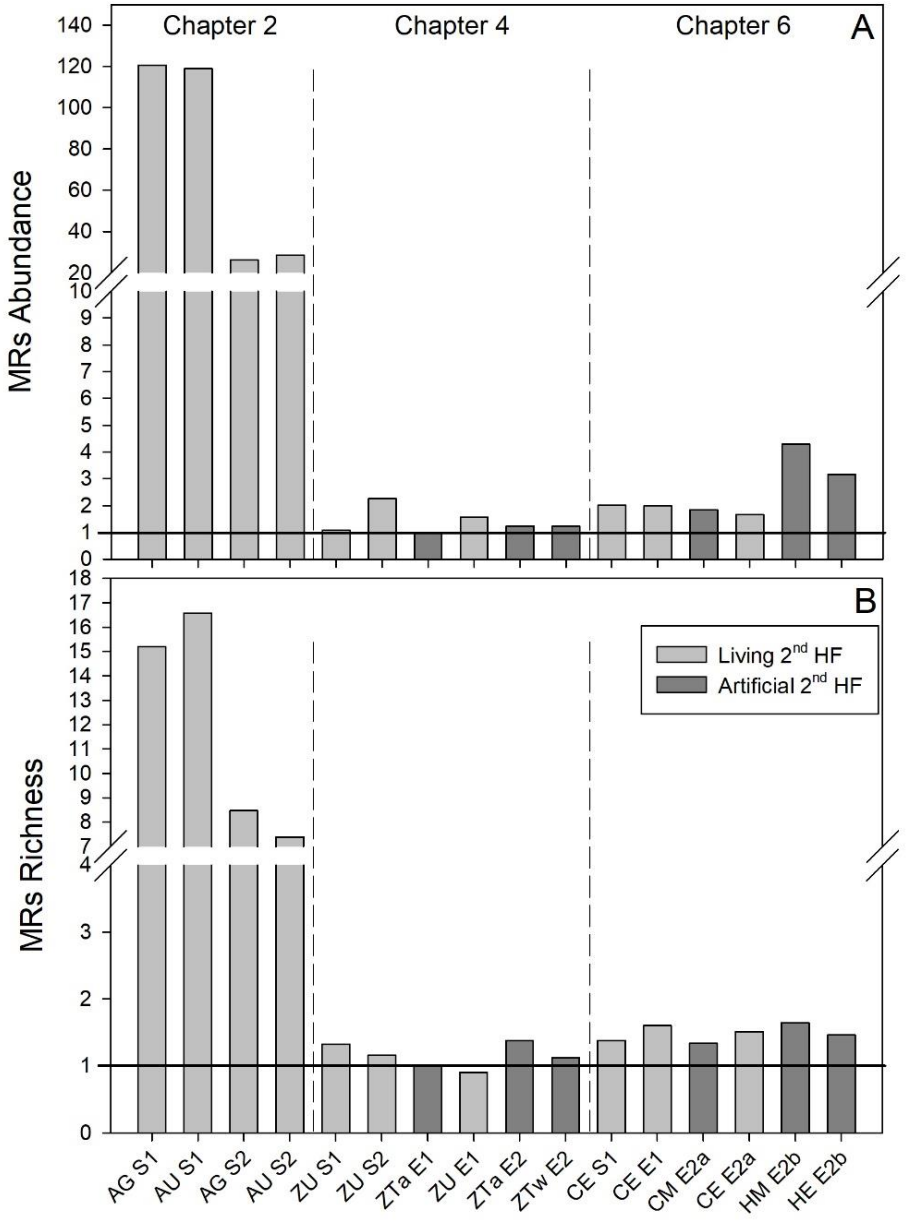
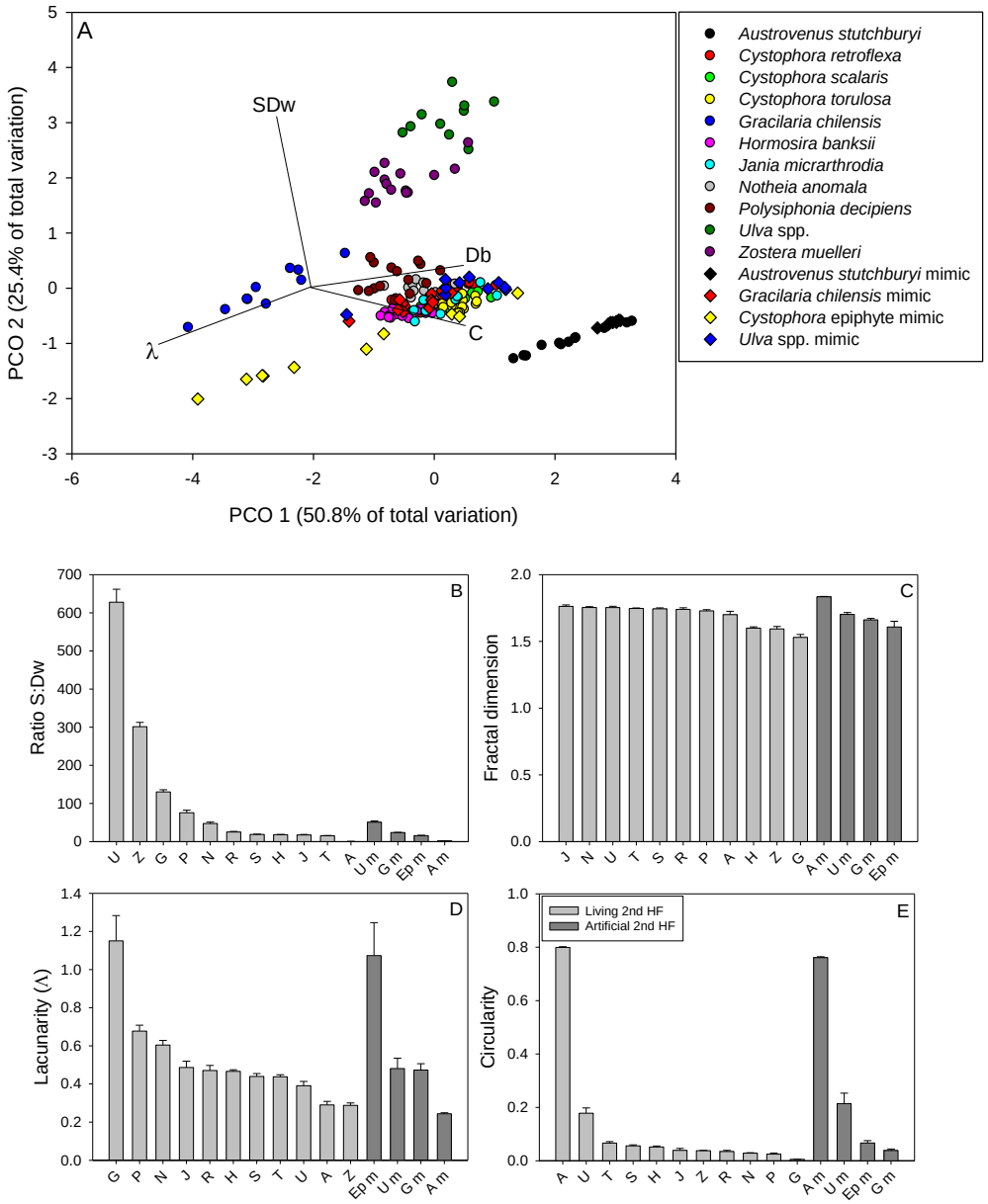


Figure 8.2 PCO analysis (A) and morphological traits (B-E) of the habitat formers investigated in this thesis (R: *Cystophora retroflexa*, S: *C. scalaris*, T: *C. torulosa*, H: *Hormosira banksii*, J: *Jania micrarthrodia*, P: *Polysiphonia decipiens*, N: *Notheia anomala*, Z: *Zostera muelleri*, G: *Gracilaria chilensis*, U: *Ulva* sp., A: *Austrovenus stutchburyi*, Ep: *Cystophora* epiphyte, m: mimic). In A, circles represent living habitat formers whereas diamonds represent mimics. n = 10. SDw: surface area:dry weight; Db: fractal dimension; C: circularity; Λ: lacunarity. Data were square-rooted and normalised prior to analysis. In B (ratio S:Dw), C (fractal dimension), D (lacunarity) and E (circularity) living habitat formers are in grey whereas artificial are in dark grey (and additionally identified with 'm' after the initial name of the species). Error bars = 1 SE, n = 10. In most of cases, error bars are too small to be visible.



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APPENDIX 1. Testing for effects of habitat-forming species on light, temperature and relative humidity

Introduction and Methods. An indoor (temperature and light controlled room) and outdoor (natural variation in light and temperature) experiments tested for effect of key habitat-forming (living or mimic) species on temperature, light and water retention, simulating a 4h low tide cycle. Ten healthy fronds of 7 different test species (*Cystophora retroflexa, C. scalaris, C. torulosa, Hormosira banksii, Zostera muelleri, Gracilaria chilensis, Ulva* sp.) were collected from either Avon-Heathcote Estuary (43°33'06.1"S, 172°44'43.3"E) or Pile Bay (43°37'05.4"S, 172°45'50.6"E). In addition, 10 similar sized mimics of habitat formers analysed in this thesis (epiphyte mimic, *Gracilaria* mimic, *Ulva* mimic) were constructed from plastic flagging tape and plastic twine. All living fronds were first acclimatized for 24h in aerated aquaria with 34 psu at 16° C in a 12:12 day length temperature controlled room to produce standard starting conditions. After acclimatization, living fronds were cut to obtain 10 pieces of three different biomasses per species (3 low, 4 medium and 3 high biomass). The experiment was run as multiple sub-experiments (it was no possible doing all species in a single setting; a sub-experiment typically included 3 species). Before starting the experiment, a concrete square block (where seaweed/seagrass frond were added onto) was saturated with seawater at room temperature (to simulate a rock after a falling tide) and a pendant Hobo light and temperature logger was placed on it (recording data at 10 minute intervals). Fronds were collected from an aquarium, drained for 3 seconds, and weighted before being placed on the concrete block to create a canopy over the Hobo logger (Table 1 for initial biomass of primary produces). Three loggers were also placed on concrete tiles without any seaweed coverage. The procedure for out-transplanting 30 samples took 20 minutes, so that the last sample was exposed to 'low tide' 20 minutes later than the first sample. I weighted the biomass of each sample after ca 0, 2 and 4 h of exposure to desiccation.

Above procedure was the same for the indoor and out-door experiment but environmental conditions for the indoor experiment were 5.90 ± 0.02 °C, 156.46 ± 2.49 Lux 16° C, and 12:12 LD, whereas conditions for the outdoor experiment were 18.12 ± 0.35 °C and 25863.96 ± 2771.16 Lux. Here, changes in biomass over time were considered an indirect measure of desiccation stress. All response variables were converted to percent change compared to the start conditions (i.e., T0 = 100%).

Results. In my thesis I evaluated how habitat-forming species affected invertebrates in habitat cascades. Here I extended this analysis by measuring how habitat formers affected abiotic conditions, to provide mechanistic insight into why inhabitants responded as they did.

Biomass reduction (proxy for desiccation stress) was strongest in the first half of the experiment (Fig. 1) after which biomass loss was much reduced (the plastic mimics only had initial water loss due to evaporation of superficial water, after which no further loss was observed). In addition, the outdoor experiment had up to 3× stronger desiccation compared to the indoor experiment. Finally, I found that samples with low biomass experienced strongest desiccation stress. More specifically, *Gracilaria* and *Zostera* had strongest desiccation (> 80% gWW loss), followed by *Cystophora* spp. (up to 70%) and *Ulva* (up to 60%).

Temperature was lower under fronds in the outdoor experiment (Fig. 2, temperature was controlled in the indoor experiment) and that high frond biomass kept temperature lower and for longer period compared to fronds in medium and low biomass. It should be noted that anomalous reduction in temperature may be due to water drops falling directly on the temperature loggers' sensor in the initial stage of the experiment (but this artefact is easy to identify because it only appeared to happen in the first 1-10 minutes after the experiment was started, e.g. Fig. 2F, 2H, 2I and 2J). I also noted that thicker habitat-forming fucoids such as *Cystophora* spp. and *Hormosira*, had strong temperature reduction in the outdoor experiment (up to ca 30%, Fig. 2A-D). As expected, I also found that *Gracilaria* buffered temperature better than *Ulva* (for *Ulva* temperature even increased for a short period of time, perhaps because of its transparent tissue). I also found that *Zostera* and the plastic mimics only had minimal impact on temperature (Fig. 2E-F).

Finally, I found that light was reduced below fronds (Fig. 3), in the laboratory from 50-100% but less in the outdoor experiment, and that high biomasses reduced light more than low biomass.

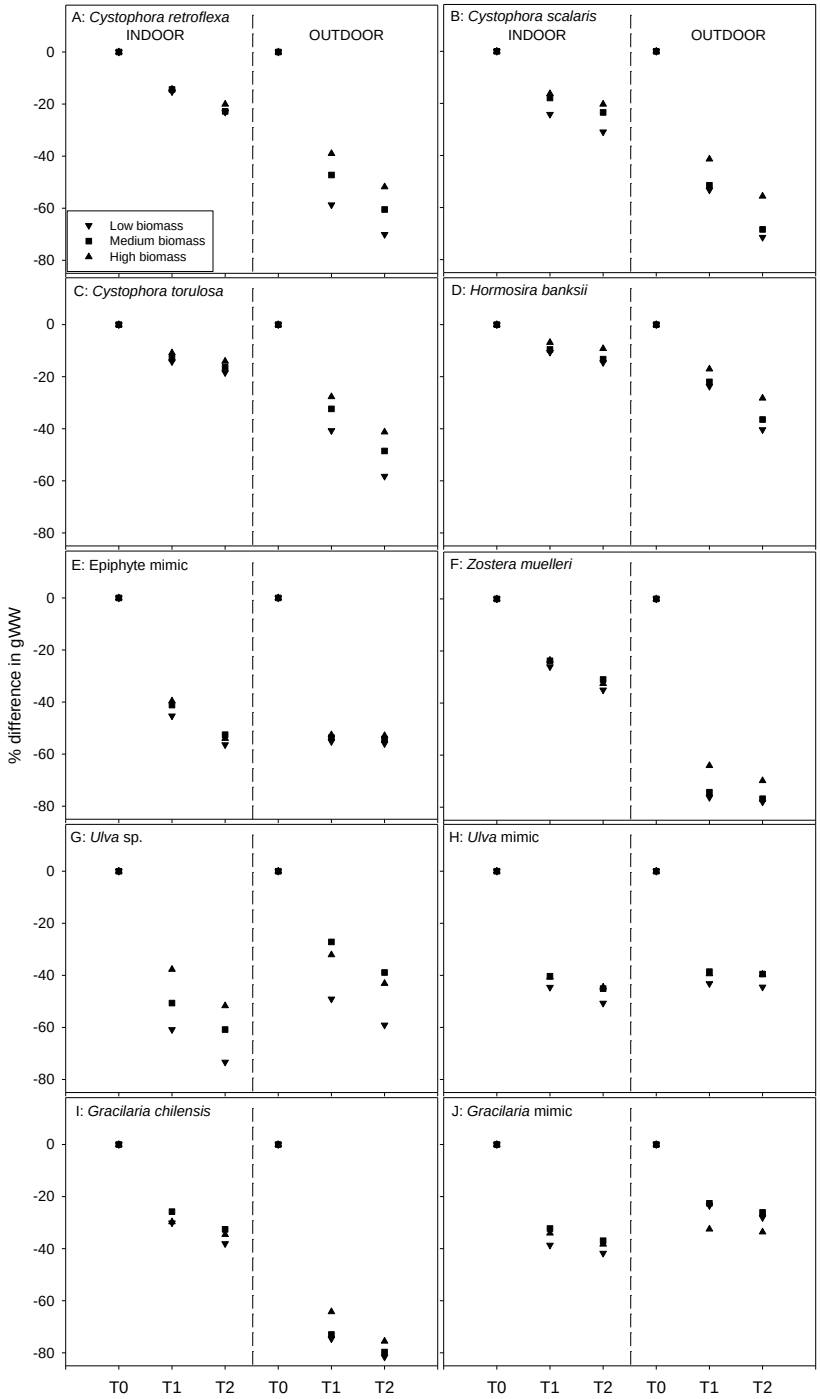
Appendix 1. Table 1

Initial biomass of primary produces (gWW ± SE) used in the indoor and outdoor experiments.

Species	Low *n* = 6	Medium *n* = 8	High *n* = 6
Cystophora retroflexa	10.90 ± 1.23	29.93 ± 1.36	73.97 ± 5.81
Cystophora scalaris	12.48 ± 0.73	37.21 ± 2.42	90.73 ± 7.96
Cystophora torulosa	15.17 ± 0.56	59.15 ± 3.83	114.99 ± 2.44
Epiphyte mimic	3.74 ± 0.28	6.84 ± 0.37	8.81 ± 0.65
Hormosira banksii	13.08 ± 0.61	39.54 ± 0.87	57.60 ± 3.78
Zostera muelleri	10.34 ± 0.43	16.47 ± 1.01	31.80 ± 0.68
Gracilaria chilensis	12.66 ± 0.35	19.89 ± 1.18	36.22 ± 1.02
Gracilaria mimic	0.73 ± 0.04	1.26 ± 0.05	2.49 ± 0.05
Ulva sp.	8.43 ± 1.39	12.49 ± 1.23	30.88 ± 6.49
Ulva mimic	2.44 ± 0.17	3.93 ± 0.21	8.04 ± 0.58

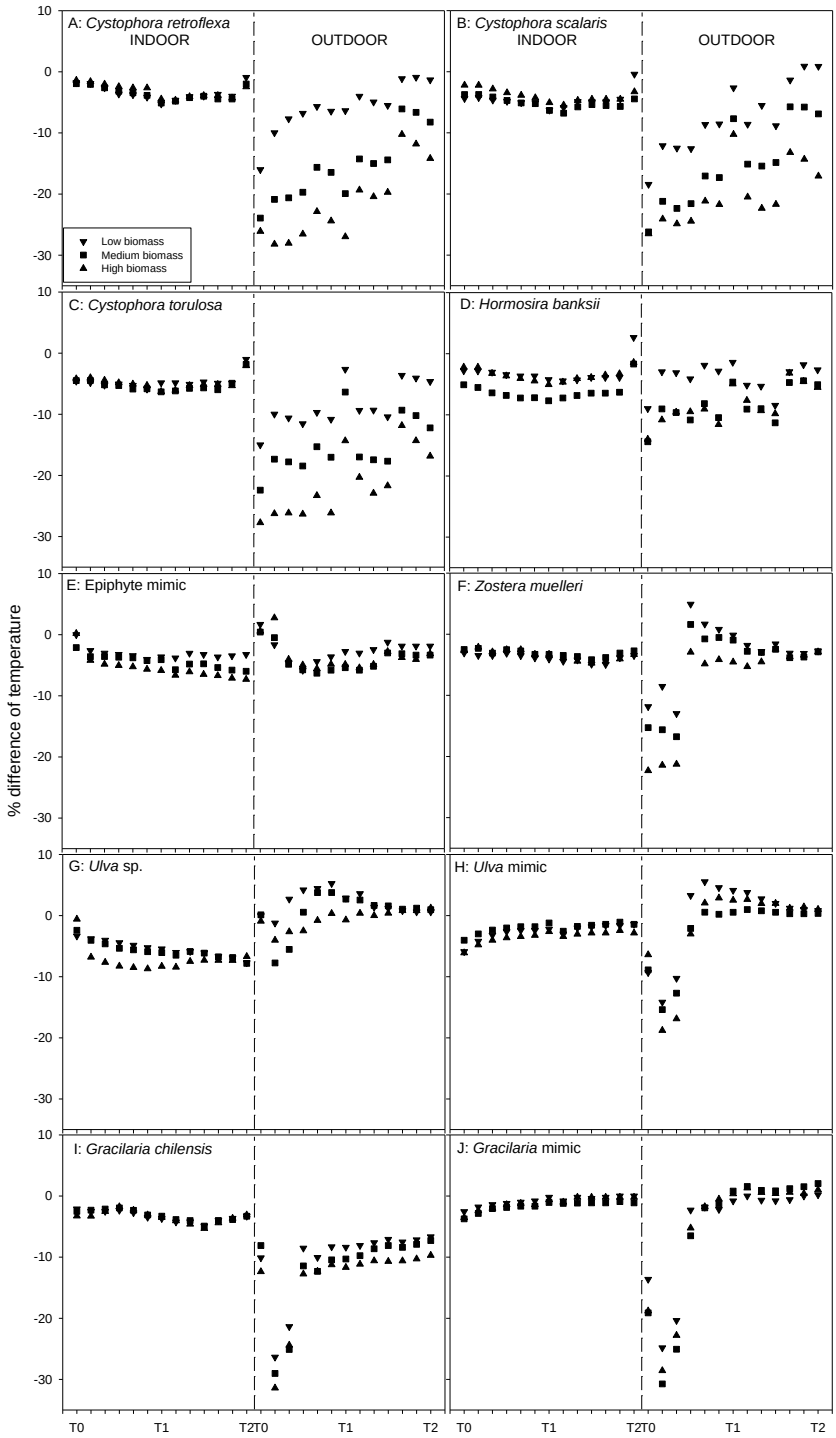
Appendix 1. Figure 1

Experiment showing percent change in seaweed biomass (gWW, an indirect measure of desiccation rate) during a simulated 4h low tide cycle indoor and outdoor. Seaweeds were out-transplanted in low (triangle down), medium (square) and high (triangle up) biomass. n = 3.



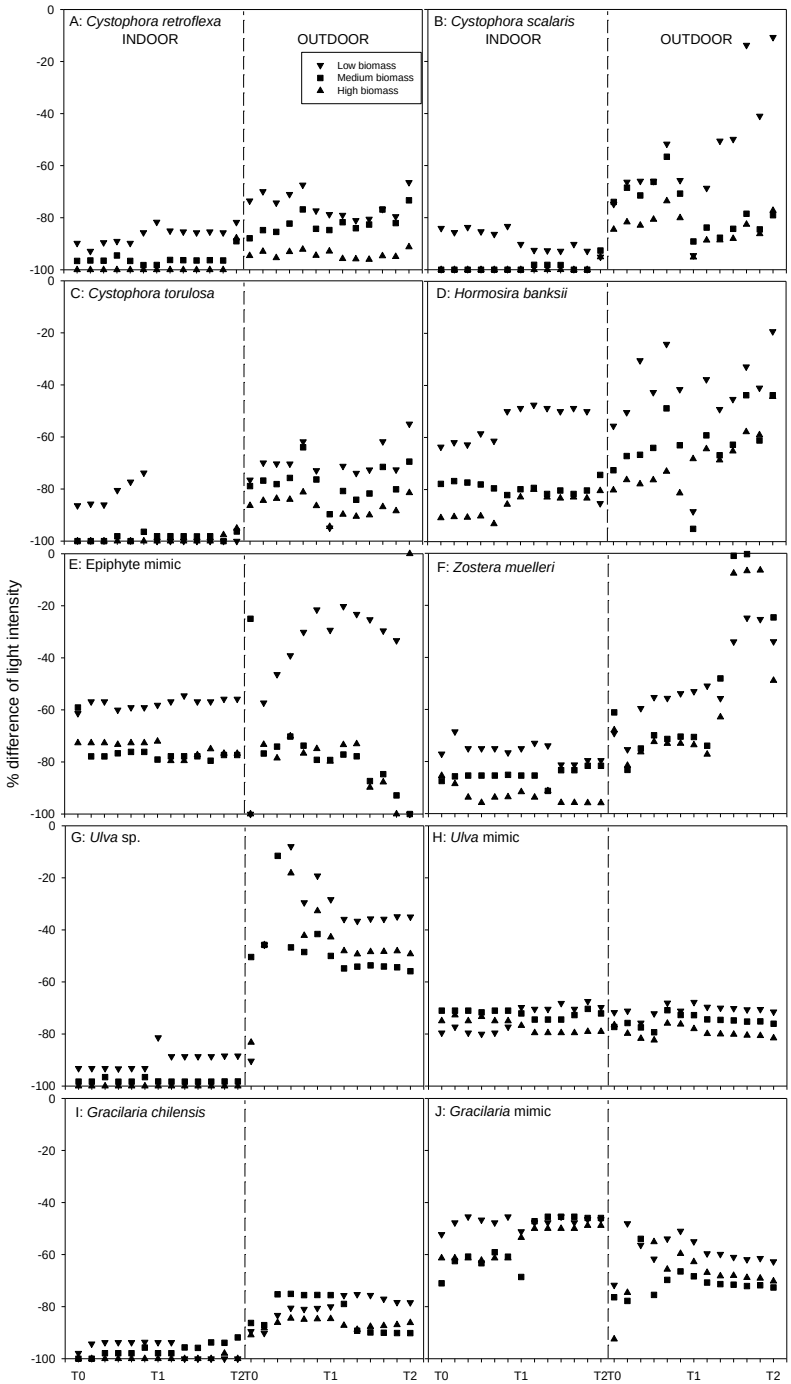
Appendix 1. Figure 2

Experiment showing percent change in temperature underneath seaweeds during a simulated 4h low tide cycle indoor and outdoor. Seaweeds were out-transplanted in low (triangle down), medium (square) and high (triangle up) biomass. n = 3.



Appendix 1. Figure 3

Experiment showing percent change in light (lux) underneath seaweeds during a simulated 4h low tide cycle indoor and outdoor. Seaweeds were out-transplanted in low (triangle down), medium (square) and high (triangle up) biomass. n = 3.



APPENDIX 2. Published paper: 'A sixth-level habitat cascade increases biodiversity in an intertidal estuary'

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ORIGINAL RESEARCH

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A sixth-level habitat cascade increases biodiversity in an intertidal estuary

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Abstract

Many studies have documented habitat cascades where two co-occurring habitat-forming species control biodiversity. However, more than two habitat-formers could theoretically co-occur. We here documented a sixth-level habitat cascade from the Avon-Heathcote Estuary, New Zealand, by correlating counts of attached inhabitants to the size and accumulated biomass of their biogenic hosts. These data revealed predictable sequences of habitat-formation (=attachment space). First, the bivalve *Austrovenus* provided habitat for green seaweeds (*Ulva*) that provided habitat for trochid snails in a typical estuarine habitat cascade. However, the trochids also provided habitat for the nonnative bryozoan *Conopeum* that provided habitat for the red seaweed *Gigartina* that provided habitat for more trochids, thereby resetting the sequence of the habitat cascade, theoretically in perpetuity. *Austrovenus* is here the basal habitat-former that controls this "long" cascade. The strength of facilitation increased with seaweed frond size, accumulated seaweed biomass, accumulated shell biomass but less with shell size. We also found that *Ulva* attached to all habitat-formers, trochids attached to *Ulva* and *Gigartina*, and *Conopeum* and *Gigartina* predominately attached to trochids. These "affinities" for different habitat-forming species probably reflect species-specific traits of juveniles and adults. Finally, manipulative experiments confirmed that the amount of seaweed and trochids was important and consistent regulators of the habitat cascade in different estuarine environments. We also interpreted this cascade as a habitat-formation network that describes the likelihood of an inhabitant being found attached to a specific habitat-former. We conclude that the strength of the cascade increased with the amount of higher-order habitat-formers, with differences in form and function between higher and lower-order habitat-formers, and with the affinity of inhabitants for higher-order habitat-formers. We suggest that long habitat cascades are common where species traits allow for physical attachment to other species, such as in marine benthic systems and old forest.

KEYWORDS
epibiosis, facilitation cascade, indirect facilitation

APPENDIX 3. Supplementary tables and figures for data chapter 2-7

Appendix 2.1

Table reporting all the estuaries and sites object of the spatial survey and the seasonal survey with GPS coordinates and replicates of the treatments (0: control *Austrovenus stutchburyi*, G: *Austrovenus stutchburyi* + *Gracilaria chilensis*, U: *Austrovenus stutchburyi* + *Ulva* sp.). Note that some estuaries do not have a proper name and I use names from the bays in which they are located.

AREA	REGION	DATES	ESTUARY	GEOCOORDINATES	SAMPLES		
					0	G	U
North	Tasman	18/04/2016	Ruataniwha Inlet	40°39'6.73S, 172°40'38.80E	4	8	6
		19/04/2016	Puponga	40°31'33.73S, 172°44'7.79E	6	12	6
	Nelson	20/04/2016	Delaware Bay	41°9'59.78S, 173°26'33.56E	6	9	12
		21/04/2016	Nelson Haven	41°13'56.81S, 173°18'38.23E	6	12	12
	Marlborough	22/04/2016	Thompson Bay	41°15'52.27S, 173°55'11.92E	6	12	12
		23/04/2016	Ngakuta Bay	41°16'19.49S, 173°57'52.03E	3	12	10
Middle	Canterbury	03/03/2015 to 10/12/2015	Avon-Heathcote Estuary - Site 1	43°33'17.5"S 172°43'16.3"E	24	24	47
		03/03/2015 to 10/12/2015	Avon-Heathcote Estuary - Site 2	43°33'16.1"S 172°43'03.2"E	24	32	48
		24/02/2016	Akaroa - Robinsons Bay	43°45'46.69S, 172°57'33.56E	6	6	9
		24/02/2016	Akaroa - Duvauchelle Bay	43°45'3.58S, 172°55'42.19E	6	12	12
		03/10/2016	Akaroa - Childrens Bay	43°47'53.18"S, 172°57'51.37"E	6	6	11
South	Otago	13/10/2016	Portobello Bay	45°49'25.25"S, 170°40'4.60"E	-	-	-
		14/10/2016	Papanui Inlet	45°50'29.50"S, 170°41'31.38"E	-	-	-
		15/10/2016	Dowling Bay	45°47'17.55"S, 170°39'50.70"E	6	6	-
	Southland	16/10/2016	Catlins River	46°28'47.31"S, 169°41'30.57"E	6	12	9
		17/10/2016	Jacobs River Estuary	46°20'53.00"S, 168° 0'55.09"E	6	9	8
		18/10/2016	New River	46°25'46.64"S, 168°20'18.40"E	-	-	-

Appendix 2.2

Spatial survey, testing for effects of identity and biomass of secondary habitat formers across latitudes. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Data were standardized per dry weight of the secondary habitat former and square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	202	22.34	**0.001**	4.83%
Biomass (Bio)	1	28	3.11	0.090	0.67%
Elevation (Ele)	1	169	18.74	**0.001**	4.06%
Latitude (Lat)	2	22	1.19	0.299	0.51%
Estuary(Latitude) (Est(Lat))	10	488	5.40	**0.001**	11.69%
Spe × Bio	1	31	3.47	0.065	0.75%
Spe × Ele	1	3	0.33	0.591	0.07%
Spe × Lat	2	100	5.54	**0.006**	2.40%
Bio × Ele	1	5	0.53	0.461	0.11%
Bio × Lat	2	42	2.32	0.109	1.00%
Ele × Lat	2	36	2.00	0.158	0.87%
Spe × Est(Lat)	9	198	2.43	**0.007**	4.74%
Bio × Est(Lat)	10	127	1.41	0.184	3.05%
Ele × Est(Lat)	9	380	4.67	**0.001**	9.09%
Spe × Bio × Ele	1	43	4.71	**0.034**	1.02%
Spe × Bio × Lat	2	18	1.00	0.366	0.43%
Spe × Ele × Lat	2	90	4.98	**0.005**	2.16%
Bio × Ele × Lat	2	67	3.68	**0.030**	1.59%
Spe × Bio × Est(Lat)	9	211	2.60	**0.011**	5.06%
Spe × Ele × Est(Lat)	5	126	2.80	**0.014**	3.03%
Bio × Ele × Est(Lat)	7	56	0.88	0.534	1.34%
Spe × Bio × Ele × Lat	2	37	2.06	0.122	0.89%
Spe × Bio × Ele × Est(Lat)	3	25	0.94	0.414	0.61%
Res	185	1673			
Total	270	4178			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	45.8	23.78	**0.001**	4.38%
Biomass (Bio)	1	254.3	132.09	**0.001**	24.34%
Elevation (Ele)	1	0.8	0.43	0.522	0.08%
Latitude (Lat)	2	27.1	7.03	**0.004**	2.59%
Estuary(Latitude) (Est(Lat))	10	71.3	3.70	**0.001**	6.83%
Spe × Bio	1	10.6	5.51	**0.013**	1.02%
Spe × Ele	1	1.0	0.50	0.472	0.09%
Spe × Lat	2	31.2	8.10	**0.002**	2.99%
Bio × Ele	1	0.7	0.35	0.553	0.06%
Bio × Lat	2	11.1	2.87	0.061	1.06%
Ele × Lat	2	1.0	0.25	0.765	0.09%
Spe × Est(Lat)	9	26.4	1.52	0.139	2.53%
Bio × Est(Lat)	10	48.0	2.49	**0.015**	4.59%
Ele × Est(Lat)	9	58.3	3.36	**0.001**	5.58%
Spe × Bio × Ele	1	0.2	0.11	0.714	0.02%
Spe × Bio × Lat	2	9.8	2.55	0.088	0.94%
Spe × Ele × Lat	2	3.6	0.95	0.403	0.35%
Bio × Ele × Lat	2	5.9	1.54	0.202	0.57%
Spe × Bio × Est(Lat)	9	28.3	1.64	0.116	2.71%
Spe × Ele × Est(Lat)	5	24.7	2.56	**0.034**	2.36%
Bio × Ele × Est(Lat)	7	12.4	0.92	0.485	1.19%
Spe × Bio × Ele × Lat	2	0.3	0.08	0.905	0.03%
Spe × Bio × Ele × Est(Lat)	3	15.8	2.74	**0.044**	1.52%
Res	185	356.1			
Total	270	1044.5			

COMMUNITY STRUCTURE					
Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Species (Spe)	1	13435	11.00	**0.001**	1.87%
Biomass (Bio)	1	25157	20.60	**0.001**	3.51%
Elevation (Ele)	1	16978	13.90	**0.001**	2.37%
Latitude (Lat)	2	49626	20.32	**0.001**	6.92%
Estuary(Latitude) (Est(Lat))	10	188160	15.41	**0.001**	26.23%
Spe × Bio	1	2079	1.70	0.116	0.29%
Spe × Ele	1	2644	2.16	**0.032**	0.37%
Spe × Lat	2	6382	2.61	**0.005**	0.89%
Bio × Ele	1	1967	1.61	0.133	0.27%
Bio × Lat	2	8236	3.37	**0.001**	1.15%
Ele × Lat	2	13164	5.39	**0.001**	1.83%
Spe × Est(Lat)	9	47838	4.35	**0.001**	6.67%
Bio × Est(Lat)	10	21564	1.77	**0.003**	3.01%
Ele × Est(Lat)	9	34591	3.15	**0.001**	4.82%
Spe × Bio × Ele	1	2002	1.64	0.138	0.28%
Spe × Bio × Lat	2	3802	1.56	0.100	0.53%
Spe × Ele × Lat	2	5133	2.10	**0.016**	0.72%
Bio × Ele × Lat	2	5947	2.43	**0.006**	0.83%
Spe × Bio × Est(Lat)	9	18709	1.70	**0.001**	2.61%
Spe × Ele × Est(Lat)	5	9458	1.55	**0.031**	1.32%
Bio × Ele × Est(Lat)	7	9505	1.11	0.309	1.32%
Spe × Bio × Ele × Lat	2	2184	0.89	0.571	0.30%
Spe × Bio × Ele × Est(Lat)	3	2911	0.79	0.710	0.41%
Res	185	225970			
Total	270	717440			

Appendix 2.3

Seasonal survey, testing for effects of identity and biomass of secondary habitat formers across seasons. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were standardized per dry weight of the secondary habitat former and square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	80.95	16.24	**0.001**	9.21%
Biomass (Bio)	1	30.03	6.02	**0.016**	3.42%
Elevation (Ele)	1	1.43	0.29	0.626	0.16%
Season (Sea)	1	0.04	0.01	0.937	0.00%
Ele × Bio	1	0.23	0.05	0.815	0.03%
Ele × Ele	1	6.48	1.30	0.276	0.74%
Ele × Sea	1	3.27	0.66	0.436	0.37%
Bio × Ele	1	4.76	0.95	0.313	0.54%
Bio × Sea	1	0.46	0.09	0.764	0.05%
Ele × Sea	1	8.64	1.73	0.176	0.98%
Ele × Bio × Ele	1	8.31	1.67	0.198	0.95%
Ele × Bio × Sea	1	5.75	1.15	0.289	0.65%
Ele × Ele × Sea	1	0.21	0.04	0.842	0.02%
Bio × Ele × Sea	1	7.75	1.55	0.206	0.88%
Ele × Bio × Ele × Sea	1	13.52	2.71	0.109	1.54%
Res	135	673.12			
Total	150	879.30			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	17.3	9.68	**0.004**	3.25%
Biomass (Bio)	1	129.1	72.18	**0.001**	24.20%
Elevation (Ele)	1	8.4	4.69	**0.028**	1.57%
Season (Sea)	1	3.9	2.16	0.150	0.72%
Ele × Bio	1	2.8	1.58	0.240	0.53%
Ele × Ele	1	0.6	0.34	0.555	0.11%
Ele × Sea	1	15.5	8.68	**0.009**	2.91%
Bio × Ele	1	8.9	4.97	**0.022**	1.67%
Bio × Sea	1	0.1	0.08	0.765	0.03%
Ele × Sea	1	9.9	5.54	**0.018**	1.86%
Ele × Bio × Ele	1	0.1	0.03	0.847	0.01%
Ele × Bio × Sea	1	7.3	4.06	**0.033**	1.36%

Ele × Ele × Sea	1	0.9	0.49	0.495	0.16%
Bio × Ele × Sea	1	3.3	1.83	0.188	0.61%
Ele × Bio × Ele × Sea	1	6.5	3.61	0.058	1.21%
Res	135	241.4			
Total	150	533.4			

COMMUNITY STRUCTURE

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Species (Spe)	1	6639	4.29	**0.001**	2.34%
Biomass (Bio)	1	12765	8.25	**0.001**	4.49%
Elevation (Ele)	1	9400	6.07	**0.001**	3.31%
Season (Sea)	1	4572	2.95	**0.004**	1.61%
Ele × Bio	1	1968	1.27	0.265	0.69%
Ele × Ele	1	4888	3.16	**0.005**	1.72%
Ele × Sea	1	3306	2.14	**0.045**	1.16%
Bio × Ele	1	1240	0.80	0.563	0.44%
Bio × Sea	1	5186	3.35	**0.004**	1.83%
Ele × Sea	1	2044	1.32	0.243	0.72%
Ele × Bio × Ele	1	863	0.56	0.775	0.30%
Ele × Bio × Sea	1	1151	0.74	0.643	0.41%
Ele × Ele × Sea	1	3742	2.42	**0.037**	1.32%
Bio × Ele × Sea	1	1373	0.89	0.516	0.48%
Ele × Bio × Ele × Sea	1	1797	1.16	0.300	0.63%
Res	135	208950			
Total	150	284100			

Appendix 2.4

Field experiment 1, testing for effects of species identity and biomass of secondary habitat-forming seaweeds across seasons. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were standardized per dry weight of the secondary habitat former and square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	6	0.61	0.435	0.22%
Biomass (Bio)	2	15	0.78	0.438	0.55%
Elevation (Ele)	1	87	9.19	**0.010**	3.24%
Site (Si)	1	15	1.59	0.228	0.56%
Season (Sea)	1	278	29.28	**0.001**	10.34%
Spe × Bio	2	0	0.01	0.991	0.00%
Spe × Ele	1	25	2.63	0.108	0.93%
Spe × Si	1	10	1.05	0.338	0.37%
Spe × Sea	1	1	0.07	0.775	0.02%
Bio × Ele	2	56	2.93	0.054	2.07%
Bio × Si	2	42	2.23	0.089	1.57%
Bio × Sea	2	175	9.21	**0.003**	6.50%
Ele × Si	1	7	0.69	0.390	0.24%
Ele × Sea	1	30	3.21	0.085	1.13%
Si × Sea	1	3	0.36	0.537	0.13%
Spe × Bio × Ele	2	24	1.26	0.273	0.89%
Spe × Bio × Si	2	71	3.77	**0.027**	2.66%
Spe × Bio × Sea	2	5	0.24	0.784	0.17%
Spe × Ele × Si	1	49	5.22	**0.026**	1.84%
Spe × Ele × Sea	1	37	3.85	0.064	1.36%
Spe × Si × Sea	1	0	0.00	0.958	0.00%
Bio × Ele × Si	2	19	0.99	0.388	0.70%
Bio × Ele × Sea	2	10	0.51	0.595	0.36%
Bio × Si × Sea	2	36	1.93	0.125	1.36%
Ele × Si × Sea	1	3	0.34	0.551	0.12%
Spe × Bio × Ele × Si	2	62	3.25	**0.048**	2.29%
Spe × Bio × Ele × Sea	2	20	1.03	0.362	0.73%
Spe × Bio × Si × Sea	2	9	0.45	0.629	0.32%
Spe × Ele × Si × Sea	1	13	1.33	0.259	0.47%
Bio × Ele × Si × Sea	2	3	0.17	0.832	0.12%
Spe × Bio × Ele × Si × Sea	1	1	0.13	0.696	0.05%

Res	148	1403
Total	194	2686

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Species (Spe)	1	16.2	3.08	0.064	1.08%
Biomass (Bio)	2	39.8	3.79	**0.035**	2.66%
Elevation (Ele)	1	57.0	10.87	**0.003**	3.82%
Site (Si)	1	26.9	5.12	**0.022**	1.80%
Season (Sea)	1	180.0	34.30	**0.001**	12.05%
Spe × Bio	2	1.1	0.11	0.906	0.07%
Spe × Ele	1	12.7	2.41	0.111	0.85%
Spe × Si	1	18.4	3.50	0.054	1.23%
Spe × Sea	1	3	0.58	0.436	0.21%
Bio × Ele	2	16	1.53	0.209	1.08%
Bio × Si	2	20	1.86	0.165	1.31%
Bio × Sea	2	113	10.77	**0.002**	7.57%
Ele × Si	1	0	0.02	0.892	0.01%
Ele × Sea	1	30	5.72	**0.024**	2.01%
Si × Sea	1	10	1.85	0.172	0.65%
Spe × Bio × Ele	2	12	1.14	0.325	0.80%
Spe × Bio × Si	2	22.8	2.17	0.110	1.53%
Spe × Bio × Sea	2	2.6	0.25	0.771	0.17%
Spe × Ele × Si	1	33.2	6.33	**0.018**	2.22%
Spe × Ele × Sea	1	16.6	3.15	0.075	1.11%
Spe × Si × Sea	1	0.4	0.09	0.768	0.03%
Bio × Ele × Si	2	13.9	1.33	0.283	0.93%
Bio × Ele × Sea	2	3.4	0.33	0.705	0.23%
Bio × Si × Sea	2	7.1	0.68	0.526	0.48%
Ele × Si × Sea	1	0.6	0.11	0.746	0.04%
Spe × Bio × Ele × Si	2	27.0	2.57	0.081	1.81%
Spe × Bio × Ele × Sea	2	7.6	0.73	0.476	0.51%
Spe × Bio × Si × Sea	2	10.7	1.02	0.384	0.71%
Spe × Ele × Si × Sea	1	2.8	0.54	0.465	0.19%
Bio × Ele × Si × Sea	2	3.1	0.30	0.734	0.21%
Spe × Bio × Ele × Si × Sea	1	4.1	0.79	0.398	0.28%
Res	148	776.8			
Total	194	1494.5			

COMMUNITY STRUCTURE					
Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Species (Spe)	1	5730	5.64	**0.002**	1.39%
Biomass (Bio)	2	21277	10.48	**0.001**	5.15%
Elevation (Ele)	1	9115	8.98	**0.001**	2.20%
Site (Si)	1	5563	5.48	**0.002**	1.35%
Season (Sea)	1	29205	28.76	**0.001**	7.06%
Spe × Bio	2	3603	1.77	0.070	0.87%
Spe × Ele	1	3621	3.57	**0.003**	0.88%
Spe × Si	1	586	0.58	0.726	0.14%
Spe × Sea	1	925	0.91	0.495	0.22%
Bio × Ele	2	5239	2.58	**0.014**	1.27%
Bio × Si	2	5614	2.76	**0.004**	1.36%
Bio × Sea	2	18474	9.10	**0.001**	4.47%
Ele × Si	1	8849	8.71	**0.001**	2.14%
Ele × Sea	1	3321	3.27	**0.004**	0.80%
Si × Sea	1	1578	1.55	0.167	0.38%
Spe × Bio × Ele	2	3408	1.68	0.090	0.82%
Spe × Bio × Si	2	8738	4.30	**0.001**	2.11%
Spe × Bio × Sea	2	2621	1.29	0.275	0.63%
Spe × Ele × Si	1	3587	3.53	**0.007**	0.87%
Spe × Ele × Sea	1	3392	3.34	**0.014**	0.82%
Spe × Si × Sea	1	652	0.64	0.706	0.16%
Bio × Ele × Si	2	2185	1.08	0.368	0.53%
Bio × Ele × Sea	2	1538	0.76	0.670	0.37%
Bio × Si × Sea	2	6665	3.28	**0.001**	1.61%
Ele × Si × Sea	1	2667	2.63	**0.019**	0.65%
Spe × Bio × Ele × Si	2	1588	0.78	0.648	0.38%
Spe × Bio × Ele × Sea	2	2125	1.05	0.374	0.51%
Spe × Bio × Si × Sea	2	3874	1.91	**0.047**	0.94%
Spe × Ele × Si × Sea	1	1387	1.37	0.255	0.34%
Bio × Ele × Si × Sea	2	4088	2.01	**0.026**	0.99%
Spe × Bio × Ele × Si × Sea	1	71	0.07	0.976	0.02%
Res	148	150280			
Total	194	413470			

Appendix 2.5

Field experiment 2, testing for structural effects vs being alive. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were standardized per dry weight of the secondary habitat former and square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
2HF type (Typ)	1	207.29	89.89	**0.001**	72.50%
2HF species (Spe)	1	0.20	0.09	0.764	0.07%
Host (Hos)	2	5.91	1.28	0.324	2.07%
Typ × Spe	1	4.83	2.09	0.168	1.69%
Typ × Hos	2	14.38	3.12	0.051	5.03%
Spe × Hos	2	3.32	0.72	0.553	1.16%
Typ × Spe × Hos	2	4.77	1.03	0.378	1.67%
Res	23	53.04			
Total	34	285.90			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
2HF type (Typ)	1	33.8	34.73	**0.001**	38.87%
2HF species (Spe)	1	2.9	2.99	0.091	3.34%
Host (Hos)	2	17.0	8.75	**0.002**	19.57%
Typ × Spe	1	1.2	1.18	0.320	1.33%
Typ × Hos	2	13.4	6.87	**0.005**	15.37%
Spe × Hos	2	5.8	3.00	0.065	6.72%
Typ × Spe × Hos	2	6.8	3.47	**0.032**	7.77%
Res	23	22.4			
Total	34	86.9			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
2HF type (Typ)	1	18005	16.72	**0.001**	29.04%
2HF species (Spe)	1	1244	1.15	0.383	2.01%
Host (Hos)	2	2714	1.26	0.241	4.38%
Typ × Spe	1	2344	2.18	**0.045**	3.78%
Typ × Hos	2	4524	2.10	**0.022**	7.30%
Spe × Hos	2	3123	1.45	0.159	5.04%
Typ × Spe × Hos	2	5190	2.41	**0.009**	8.37%
Res	23	24773			
Total	34	62008			

Appendix 2.6

Experiment 3, predation experiment. Chi-square test based on the distribution of *Micrelenchus tenebrosus* in different habitats (M: mud, U: *Ulva* sp., G: *Gracilaria chilensis*) and in absence (N) and presence (Y) of the predator. The expected frequencies values took into account the snails missing during the experiments (i.e., values are slightly different across habitats and predation conditions).

OBSERVED FREQUENCIES TABLE

HABITAT	CRAB PRESENCE	M	U	G	TOT
M	**N**	10.33	0.00	0.00	10.33
M	**Y**	13.00	0.00	0.00	13.00
MU	**N**	5.00	7.33	0.00	12.33
MU	**Y**	3.17	8.83	0.00	12.00
MG	**N**	9.83	0.00	3.50	13.33
MG	**Y**	7.33	0.00	4.50	11.83
TOT		48.67	16.17	8.00	72.83
PROP		0.67	0.22	0.11	1.00

EXPECTED FREQUENCIES TABLE

HABITAT	CRAB PRESENCE	M	U	G
M	**N**	6.90	2.29	1.14
M	**Y**	8.69	2.89	1.43
MU	**N**	8.24	2.74	1.35
MU	**Y**	8.02	2.66	1.32
MG	**N**	8.91	2.96	1.46
MG	**Y**	7.91	2.63	1.30

Chi Test	**1E-08**

Appendix 2.7

Field experiment 2, experimental treatments. Fig. A, left to right: living *Austrovenus stutchburyi*, *Austrovenus* shell, *Austrovenus* mimic. Fig. B, left to right: *Austrovenus* mimic + *Ulva* mimic, *Austrovenus* shell + *Ulva* mimic, living *Austrovenus* + living *Ulva*, *Austrovenus* mimic + *Gracilaria* mimic, *Austrovenus* shell + *Gracilaria* mimic, living *Austrovenus* + living *Gracilaria*. The *Austrovenus* mimic were 3D printed (three different sizes: 30, 32, 35 mm length). *Gracilaria* and *Ulva* mimics were made from plastic twine and tape, respectively (20 cm length, 1.60 and 1.50 gDW).

Appendix 3.1

Observational study. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	1373	3.65	**0.050**	2.81%
***Gracilaria* biomass (Bio)**	1	16433	43.67	**0.001**	33.62%
Site (Si)	1	49	0.13	0.725	0.10%
Season (Sea)	1	525	1.39	0.225	1.07%
Ulv × Bio	1	163	0.43	0.521	0.33%
Ulv × Si	1	987	2.62	0.110	2.02%
Ulv × Sea	1	455	1.21	0.267	0.93%
Bio × Si	1	13	0.03	0.864	0.03%
Bio × Sea	1	480	1.28	0.261	0.98%
Si × Sea	1	622	1.65	0.212	1.27%
Ulv × Bio × Si	1	174	0.46	0.491	0.36%
Ulv × Bio × Sea	1	405	1.08	0.317	0.83%
Ulv × Si × Sea	1	135	0.36	0.576	0.28%
Bio × Si × Sea	1	695	1.85	0.162	1.42%
Ulv × Bio × Si × Sea	1	30	0.08	0.772	0.06%
Res	70	26344			
Total	85	48883			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	0	0.08	0.792	0.07%
***Gracilaria* biomass (Bio)**	1	33	10.41	**0.005**	9.48%
Site (Si)	1	15	4.73	**0.025**	4.31%
Season (Sea)	1	25	7.82	**0.007**	7.13%
Ulv × Bio	1	6	1.82	0.171	1.66%
Ulv × Si	1	14	4.35	**0.043**	3.96%
Ulv × Sea	1	0	0.07	0.817	0.06%
Bio × Si	1	7	2.10	0.160	1.91%
Bio × Sea	1	6	2.02	0.164	1.84%
Si × Sea	1	0	0.10	0.750	0.09%
Ulv × Bio × Si	1	7	2.11	0.151	1.93%
Ulv × Bio × Sea	1	9	2.86	0.100	2.61%
Ulv × Si × Sea	1	2	0.70	0.397	0.64%

Bio × Si × Sea	1	2	0.49	0.519	0.45%
Ulv × Bio × Si × Sea	1	0	0.08	0.774	0.08%
Res	70	225			
Total	85	353			

COMMUNITY STRUCTURE

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
***Ulva* (Ulv)**	1	7233	5.61	**0.001**	5.35%
***Gracilaria* biomass (Bio)**	1	11232	8.71	**0.001**	8.30%
Site (Si)	1	5423	4.20	**0.001**	4.01%
Season (Sea)	1	3951	3.06	**0.012**	2.92%
Ulv × Bio	1	1666	1.29	0.261	1.23%
Ulv × Si	1	4449	3.45	**0.001**	3.29%
Ulv × Sea	1	2052	1.59	0.160	1.52%
Bio × Si	1	1471	1.14	0.331	1.09%
Bio × Sea	1	996	0.77	0.585	0.74%
Si × Sea	1	575	0.45	0.860	0.43%
Ulv × Bio × Si	1	1543	1.20	0.320	1.14%
Ulv × Bio × Sea	1	1880	1.46	0.217	1.39%
Ulv × Si × Sea	1	910	0.71	0.645	0.67%
Bio × Si × Sea	1	892	0.69	0.655	0.66%
Ulv × Bio × Si × Sea	1	708	0.55	0.766	0.52%
Res	70	90312			
Total	85	135290			

Appendix 3.2

Manipulative experiment. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	57	0.14	0.712	0.63%
Elevation (Ele)	1	63	0.16	0.684	0.70%
Site (Si)	1	442	1.10	0.325	4.89%
Ulv × Ele	1	126	0.31	0.614	1.39%
Ulv × Si	1	925	2.30	0.155	10.23%
Ele × Si	1	35	0.09	0.768	0.39%
Ulv × Ele × Si	1	950	2.36	0.145	10.51%
Res	16	6443			
Total	23	9042			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	0.03	1.63	0.191	5.33%
Elevation (Ele)	1	0.01	0.72	0.400	2.35%
Site (Si)	1	0.08	4.70	0.052	15.35%
Ulv × Ele	1	0.00	0.21	0.642	0.68%
Ulv × Si	1	0.00	0.06	0.807	0.19%
Ele × Si	1	0.03	1.82	0.185	5.94%
Ulv × Ele × Si	1	0.10	5.50	**0.027**	17.94%
Res	16	0.28			
Total	23	0.54			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	1710	1.62	0.191	5.17%
Elevation (Ele)	1	1327	1.26	0.306	4.01%
Site (Si)	1	610	0.58	0.626	1.84%
Ulv × Ele	1	1922	1.82	0.159	5.81%
Ulv × Si	1	2415	2.29	0.083	7.30%
Ele × Si	1	4575	4.34	**0.008**	13.84%
Ulv × Ele × Si	1	3616	3.43	**0.026**	10.94%
Res	16	16884			
Total	23	33059			

Appendix 3.3

Natural experiment. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were square-root transformed.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	725	6.06	**0.015**	7.65%
Habitat (Hab)	1	96	0.80	0.386	1.01%
Estuary (Est)	2	1563	6.54	**0.006**	16.49%
Ulv × Hab	1	265	2.22	0.162	2.80%
Ulv × Est	2	260	1.09	0.349	2.74%
Hab × Est	2	178	0.74	0.467	1.88%
Ulv × Hab × Est	2	55	0.23	0.797	0.58%
Res	53	6336			
Total	64	9479			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	0.29	1.92	0.168	1.88%
Habitat (Hab)	1	1.00	6.73	**0.017**	6.59%
Estuary (Est)	2	4.14	13.90	**0.001**	27.23%
Ulv × Hab	1	0.07	0.47	0.480	0.46%
Ulv × Est	2	0.34	1.14	0.331	2.24%
Hab × Est	2	0.15	0.51	0.595	1.00%
Ulv × Hab × Est	2	1.32	4.44	**0.023**	8.69%
Res	53	7.90			
Total	64	15.21			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
***Ulva* (Ulv)**	1	4410	2.67	**0.010**	3.29%
Habitat (Hab)	1	3627	2.20	**0.028**	2.71%
Estuary (Est)	2	26212	7.95	**0.001**	19.57%
Ulv × Hab	1	1427	0.87	0.532	1.06%
Ulv × Est	2	3515	1.07	0.383	2.62%
Hab × Est	2	3152	0.96	0.492	2.35%
Ulv × Hab × Est	2	4243	1.29	0.235	3.17%
Res	53	87369			
Total	64	133950			

Appendix 4.1

Overview data of surveyed estuaries and sites and number of replicated cores (samples) collected with and without different types of habitat formers: mud (M), *Ulva* sp. (U), *Gracilaria chilensis* (G), *Lophothamnion hirtum* (L), *Zostera muelleri* (Z), *Zostera* + *Ulva* (ZU), *Zostera* + *Gracilaria* (ZG), *Zostera* + *Lophothamnion* (ZL), *Zostera* + *Polysiphonia* sp. (ZP).

AREA	REGION	DATES	ESTUARY	GEOCOORDINATES	SAMPLES								
					M	U	G	L	Z	ZU	ZG	ZL	ZP
North	Tasman	18/04/2016	Ruataniwha Inlet	40°39'6.73S, 172°40'38.80E	6	6	3	-	6	6	3	-	-
		19/04/2016	Puponga	40°31'33.73S, 172°44'7.79E	6	3	3	-	6	-	-	-	3
	Nelson	20/04/2016	Delaware Bay	41°9'59.78S, 173°26'33.56E	6	6	-	-	6	6	-	-	-
		21/04/2016	Nelson Haven	41°13'56.81S, 173°18'38.23E	6	6	6	-	6	6	-	-	-
	Marlborough	22/04/2016	Thompson Bay	41°15'52.27S, 173°55'11.92E	6	6	6	-	6	6	-	-	-
		23/04/2016	Ngakuta Bay	41°16'19.49S, 173°57'52.03E	6	6	6	-	6	6	-	-	-
Middle	Canterbury	04/12/2014 to 11/03/2015	Avon-Heathcote Estuary - Site 1	43°33'19.78"S, 172°43'16.81"E	32	32	-	-	32	32	-	-	-
		04/12/2014 to 11/03/2015	Avon-Heathcote Estuary - Site 2	43°33'17.32"S, 172°43'3.50"E	32	32	-	-	32	33	-	-	-
		24/02/2016	Akaroa - Robinsons Bay	43°45'46.69S, 172°57'33.56E	6	-	-	-	6	4	2	-	-
		24/02/2016	Akaroa - Duvauchelle Bay	43°45'3.58S, 172°55'42.19E	6	-	-	-	10	-	2	-	-
		03/10/2016	Akaroa - Childrens Bay	43°47'53.18"S, 172°57'51.37"E	6	-	-	6	6	-	-	6	-
		13/10/2016	Portobello Bay	45°49'25.25"S, 170°40'4.60"E	6	6	-	-	6	6	-	-	-
South	Otago	14/10/2016	Papanui Inlet	45°50'29.50"S, 170°41'31.38"E	6	6	-	-	6	6	-	-	-
		15/10/2016	Dowling Bay	45°47'17.55"S, 170°39'50.70"E	6	6	-	-	6	6	-	-	-
		16/10/2016	Catlins River	46°28'47.31"S, 169°41'30.57"E	6	6	-	-	6	6	-	-	-
	Southland	17/10/2016	Jacobs River Estuary	46°20'53.00"S, 168° 0'55.09"E	6	12	6	-	6	12	6	-	-
		18/10/2016	New River	46°25'46.64"S, 168°20'18.40"E	3	3	6	-	6	1	6	-	-

Appendix 4.2

Spatial survey, effects of secondary habitat former across latitudes. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Data were square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	125.04	122.74	**0.001**	8.00%
Primary habitat former (1HF)	1	87.94	86.32	**0.001**	5.62%
Elevation (Ele)	1	0.51	0.50	0.501	0.03%
Latitude (Lat)	2	31.41	15.42	**0.001**	2.01%
Estuary(Latitude) (Est(Lat))	13	734.78	55.48	**0.001**	47.00%
2HF × 1HF	1	4.52	4.44	**0.035**	0.29%
2HF × Ele	1	0.00	0.00	0.949	0.00%
2HF × Lat	2	42.88	21.04	**0.001**	2.74%
1HF × Ele	1	2.11	2.07	0.161	0.13%
1HF × Lat	2	7.11	3.49	**0.036**	0.46%
Ele × Lat	2	5.39	2.65	0.082	0.34%
2HF × Est(Lat)	13	72.15	5.45	**0.001**	4.61%
1HF × Est(Lat)	13	30.65	2.31	**0.004**	1.96%
Ele × Est(Lat)	13	26.22	1.98	**0.023**	1.68%
2HF × 1HF × Ele	1	0.28	0.27	0.595	0.02%
2HF × 1HF × Lat	2	7.11	3.49	**0.031**	0.45%
2HF × Ele × Lat	2	1.04	0.51	0.590	0.07%
1HF × Ele × Lat	2	0.01	0.01	0.995	0.00%
2HF × 1HF × Est(Lat)	11	9.12	0.81	0.614	0.58%
2HF × Ele × Est(Lat)	12	13.30	1.09	0.361	0.85%
1HF × Ele × Est(Lat)	13	11.12	0.84	0.587	0.71%
2HF × 1HF × Ele × Lat	2	4.44	2.18	0.145	0.28%
2HF × 1HF × Ele × Est(Lat)	9	2.91	0.32	0.975	0.19%
Res	337	343.32			
Total	457	1563.40			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	10.24	65.25	**0.001**	7.33%
Primary habitat former (1HF)	1	6.10	38.85	**0.001**	4.36%
Elevation (Ele)	1	0.64	4.05	**0.039**	0.45%
Latitude (Lat)	2	21.68	69.08	**0.001**	15.52%
Estuary(Latitude) (Est(Lat))	13	27.62	13.54	**0.001**	19.77%
2HF × 1HF	1	0.18	1.16	0.285	0.13%
2HF × Ele	1	0.04	0.24	0.622	0.03%
2HF × Lat	2	1.02	3.25	**0.042**	0.73%
1HF × Ele	1	0.04	0.24	0.615	0.03%
1HF × Lat	2	0.74	2.37	0.107	0.53%
Ele × Lat	2	0.30	0.94	0.378	0.21%
2HF × Est(Lat)	13	2.35	1.15	0.336	1.68%
1HF × Est(Lat)	13	4.62	2.27	**0.004**	3.31%
Ele × Est(Lat)	13	4.20	2.06	**0.015**	3.00%
2HF × 1HF × Ele	1	0.00	0.01	0.928	0.00%
2HF × 1HF × Lat	2	0.00	0.00	0.994	0.00%
2HF × Ele × Lat	2	0.61	1.96	0.148	0.44%
1HF × Ele × Lat	2	0.56	1.79	0.179	0.40%
2HF × 1HF × Est(Lat)	11	0.48	0.28	0.988	0.34%
2HF × Ele × Est(Lat)	12	1.23	0.66	0.808	0.88%
1HF × Ele × Est(Lat)	13	2.94	1.44	0.149	2.10%
2HF × 1HF × Ele × Lat	2	0.01	0.02	0.975	0.00%
2HF × 1HF × Ele × Est(Lat)	9	1.26	0.89	0.553	0.90%
Res	337	52.88			
Total	457	139.72			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	17493	18.73	**0.001**	1.67%
Primary habitat former (1HF)	1	15520	16.62	**0.001**	1.48%
Elevation (Ele)	1	5394	5.77	**0.001**	0.51%
Latitude (Lat)	2	122640	65.65	**0.001**	11.70%
Estuary(Latitude) (Est(Lat))	13	361780	29.79	**0.001**	34.52%
2HF × 1HF	1	5700	6.10	**0.001**	0.54%
2HF × Ele	1	1419	1.52	0.181	0.14%
2HF × Lat	2	9240	4.95	**0.001**	0.88%
1HF × Ele	1	2171	2.32	**0.036**	0.21%
1HF × Lat	2	4855	2.60	**0.003**	0.46%
Ele × Lat	2	9772	5.23	**0.001**	0.93%
2HF × Est(Lat)	13	32172	2.65	**0.001**	3.07%
1HF × Est(Lat)	13	37517	3.09	**0.001**	3.58%
Ele × Est(Lat)	13	34254	2.82	**0.001**	3.27%
2HF × 1HF × Ele	1	73	0.08	0.966	0.01%
2HF × 1HF × Lat	2	4380	2.34	**0.004**	0.42%
2HF × Ele × Lat	2	2279	1.22	0.289	0.22%
1HF × Ele × Lat	2	3017	1.61	0.094	0.29%
2HF × 1HF × Est(Lat)	11	17721	1.72	**0.001**	1.69%
2HF × Ele × Est(Lat)	12	12750	1.14	0.232	1.22%
1HF × Ele × Est(Lat)	13	22508	1.85	**0.001**	2.15%
2HF × 1HF × Ele × Lat	2	2658	1.42	0.178	0.25%
2HF × 1HF × Ele × Est(Lat)	9	7921	0.94	0.587	0.76%
Res	337	314800			
Total	457	1048000			

Appendix 4.3

Seasonal survey, effects of secondary habitat formers across seasons. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	466.82	227.59	**0.001**	31.27%
Primary habitat former (1HF)	1	172.10	83.91	**0.001**	11.53%
Elevation (Ele)	1	32.06	15.63	**0.001**	2.15%
Site (Si)	1	0.08	0.04	0.831	0.01%
Season (Sea)	1	94.24	45.94	**0.001**	6.31%
Year (Yea)	1	55.79	27.20	**0.001**	3.74%
2HF × 1HF	1	7.44	3.63	0.059	0.50%
2HF × Ele	1	1.64	0.80	0.367	0.11%
2HF × Si	1	0.37	0.18	0.668	0.02%
2HF × Sea	1	67.98	33.15	**0.001**	4.55%
2HF × Yea	1	5.62	2.74	0.091	0.38%
1HF × Ele	1	1.39	0.68	0.425	0.09%
1HF × Si	1	5.49	2.68	0.090	0.37%
1HF × Sea	1	1.28	0.63	0.433	0.09%
1HF × Yea	1	1.20	0.58	0.451	0.08%
Ele × Si	1	32.81	15.99	**0.001**	2.20%
Ele × Sea	1	0.02	0.01	0.922	0.00%
Ele × Yea	1	1.60	0.78	0.376	0.11%
Si × Sea	1	4.19	2.04	0.140	0.28%
Si × Yea	1	0.60	0.29	0.615	0.04%
Sea × Yea	1	0.02	0.01	0.936	0.00%
2HF × 1HF × Ele	1	1.00	0.49	0.482	0.07%
2HF × 1HF × Si	1	2.87	1.40	0.261	0.19%
2HF × 1HF × Sea	1	15.19	7.41	**0.006**	1.02%
2HF × 1HF × Yea	1	5.91	2.88	0.086	0.40%
2HF × Ele × Si	1	8.75	4.26	**0.044**	0.59%
2HF × Ele × Sea	1	2.54	1.24	0.287	0.17%
2HF × Ele × Yea	1	0.05	0.02	0.868	0.00%
2HF × Si × Sea	1	4.15	2.03	0.150	0.28%
2HF × Si × Yea	1	2.50	1.22	0.288	0.17%
2HF × Sea × Yea	1	4.74	2.31	0.122	0.32%
1HF × Ele × Si	1	10.86	5.29	**0.025**	0.73%

1HF × Ele × Sea	1	0.49	0.24	0.640	0.03%
1HF × Ele × Yea	1	1.56	0.76	0.396	0.10%
1HF × Si × Sea	1	9.03	4.40	**0.031**	0.60%
1HF × Si × Yea	1	0.00	0.00	0.990	0.00%
1HF × Sea × Yea	1	12.37	6.03	**0.007**	0.83%
Ele × Si × Sea	1	2.91	1.42	0.252	0.19%
Ele × Si × Yea	1	8.57	4.18	**0.045**	0.57%
Ele × Sea × Yea	1	6.97	3.40	0.068	0.47%
Si × Sea × Yea	1	1.53	0.74	0.365	0.10%
2HF × 1HF × Ele × Si	1	5.27	2.57	0.111	0.35%
2HF × 1HF × Ele × Sea	1	0.87	0.42	0.499	0.06%
2HF × 1HF × Ele × Yea	1	0.60	0.29	0.589	0.04%
2HF × 1HF × Si × Sea	1	0.01	0.00	0.960	0.00%
2HF × 1HF × Si × Yea	1	0.53	0.26	0.620	0.04%
2HF × 1HF × Sea × Yea	1	12.43	6.06	**0.012**	0.83%
2HF × Ele × Si × Sea	1	4.75	2.32	0.140	0.32%
2HF × Ele × Si × Yea	1	4.10	2.00	0.163	0.27%
2HF × Ele × Sea × Yea	1	0.39	0.19	0.628	0.03%
2HF × Si × Sea × Yea	1	4.85	2.36	0.138	0.32%
1HF × Ele × Si × Sea	1	0.32	0.16	0.687	0.02%
1HF × Ele × Si × Yea	1	0.62	0.30	0.574	0.04%
1HF × Ele × Sea × Yea	1	0.07	0.04	0.865	0.00%
1HF × Si × Sea × Yea	1	0.33	0.16	0.695	0.02%
Ele × Si × Sea × Yea	1	0.01	0.00	0.958	0.00%
2HF × 1HF × Ele × Si × Sea	1	0.01	0.00	0.939	0.00%
2HF × 1HF × Ele × Si × Yea	1	2.00	0.97	0.345	0.13%
2HF × 1HF × Ele × Sea × Yea	1	1.05	0.51	0.476	0.07%
2HF × 1HF × Si × Sea × Yea	1	4.95	2.41	0.118	0.33%
2HF × Ele × Si × Sea × Yea	1	4.35	2.12	0.148	0.29%
1HF × Ele × Si × Sea × Yea	1	1.02	0.50	0.504	0.07%
2HF × 1HF × Ele × Si × Sea × Yea	1	0.04	0.02	0.890	0.00%
Res	190	389.71			
Total	253	1493.00			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	4.03	24.21	**0.001**	6.37%
Primary habitat former (1HF)	1	3.51	21.06	**0.001**	5.54%
Elevation (Ele)	1	0.05	0.28	0.594	0.07%
Site (Si)	1	0.15	0.88	0.351	0.23%
Season (Sea)	1	0.40	2.38	0.135	0.62%
Year (Yea)	1	5.62	33.78	**0.001**	8.88%
2HF × 1HF	1	0.45	2.68	0.095	0.71%
2HF × Ele	1	0.00	0.00	0.976	0.00%
2HF × Si	1	0.16	0.94	0.331	0.25%
2HF × Sea	1	0.01	0.07	0.810	0.02%
2HF × Yea	1	0.16	0.95	0.323	0.25%
1HF × Ele	1	0.00	0.00	0.986	0.00%
1HF × Si	1	0.02	0.15	0.694	0.04%
1HF × Sea	1	0.40	2.37	0.122	0.62%
1HF × Yea	1	1.76	10.59	**0.001**	2.78%
Ele × Si	1	1.70	10.20	**0.003**	2.68%
Ele × Sea	1	0.10	0.61	0.418	0.16%
Ele × Yea	1	1.18	7.08	**0.007**	1.86%
Si × Sea	1	0.00	0.03	0.862	0.01%
Si × Yea	1	0.36	2.19	0.142	0.58%
Sea × Yea	1	5.74	34.51	**0.001**	9.08%
2HF × 1HF × Ele	1	0.00	0.02	0.899	0.01%
2HF × 1HF × Si	1	0.00	0.03	0.876	0.01%
2HF × 1HF × Sea	1	0.04	0.27	0.583	0.07%
2HF × 1HF × Yea	1	0.36	2.19	0.136	0.58%
2HF × Ele × Si	1	0.15	0.88	0.329	0.23%
2HF × Ele × Sea	1	0.00	0.03	0.868	0.01%
2HF × Ele × Yea	1	0.00	0.01	0.919	0.00%
2HF × Si × Sea	1	0.23	1.35	0.243	0.36%
2HF × Si × Yea	1	0.11	0.64	0.446	0.17%
2HF × Sea × Yea	1	0.01	0.03	0.867	0.01%
1HF × Ele × Si	1	0.35	2.09	0.162	0.55%
1HF × Ele × Sea	1	0.12	0.75	0.400	0.20%
1HF × Ele × Yea	1	0.10	0.62	0.423	0.16%
1HF × Si × Sea	1	0.02	0.09	0.764	0.02%
1HF × Si × Yea	1	0.02	0.12	0.748	0.03%
1HF × Sea × Yea	1	0.01	0.04	0.849	0.01%
Ele × Si × Sea	1	0.83	4.97	**0.026**	1.31%
Ele × Si × Yea	1	0.96	5.75	**0.020**	1.51%
Ele × Sea × Yea	1	0.03	0.19	0.660	0.05%
Si × Sea × Yea	1	0.30	1.80	0.200	0.47%
2HF × 1HF × Ele × Si	1	0.01	0.04	0.857	0.01%

2HF × 1HF × Ele × Sea	1	0.19	1.13	0.302	0.30%
2HF × 1HF × Ele × Yea	1	0.00	0.01	0.919	0.00%
2HF × 1HF × Si × Sea	1	0.53	3.19	0.077	0.84%
2HF × 1HF × Si × Yea	1	0.01	0.08	0.767	0.02%
2HF × 1HF × Sea × Yea	1	0.00	0.01	0.944	0.00%
2HF × Ele × Si × Sea	1	0.25	1.51	0.217	0.40%
2HF × Ele × Si × Yea	1	0.02	0.15	0.705	0.04%
2HF × Ele × Sea × Yea	1	0.04	0.25	0.620	0.06%
2HF × Si × Sea × Yea	1	0.04	0.21	0.627	0.06%
1HF × Ele × Si × Sea	1	0.03	0.20	0.651	0.05%
1HF × Ele × Si × Yea	1	0.13	0.79	0.368	0.21%
1HF × Ele × Sea × Yea	1	0.09	0.56	0.456	0.15%
1HF × Si × Sea × Yea	1	0.35	2.08	0.141	0.55%
Ele × Si × Sea × Yea	1	0.02	0.12	0.706	0.03%
2HF × 1HF × Ele × Si × Sea	1	0.01	0.07	0.784	0.02%
2HF × 1HF × Ele × Si × Yea	1	0.18	1.06	0.302	0.28%
2HF × 1HF × Ele × Sea × Yea	1	0.14	0.86	0.380	0.23%
2HF × 1HF × Si × Sea × Yea	1	0.01	0.08	0.751	0.02%
2HF × Ele × Si × Sea × Yea	1	0.02	0.14	0.695	0.04%
1HF × Ele × Si × Sea × Yea	1	0.09	0.55	0.459	0.14%
2HF × 1HF × Ele × Si × Sea × Yea	1	0.06	0.34	0.582	0.09%
Res	190	31.62			
Total	253	63.29			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	43971.00	43.72	**0.001**	10.54%
Primary habitat former (1HF)	1	28298.00	28.14	**0.001**	6.78%
Elevation (Ele)	1	7297.70	7.26	**0.001**	1.75%
Site (Si)	1	6834.50	6.80	**0.001**	1.64%
Season (Sea)	1	23543.00	23.41	**0.001**	5.64%
Year (Yea)	1	13939.00	13.86	**0.001**	3.34%
2HF × 1HF	1	9562.70	9.51	**0.001**	2.29%
2HF × Ele	1	354.86	0.35	0.867	0.09%
2HF × Si	1	602.54	0.60	0.702	0.14%
2HF × Sea	1	4488.90	4.46	**0.001**	1.08%
2HF × Yea	1	807.54	0.80	0.591	0.19%
1HF × Ele	1	3537.40	3.52	**0.002**	0.85%
1HF × Si	1	1798.70	1.79	0.139	0.43%
1HF × Sea	1	2349.70	2.34	**0.030**	0.56%
1HF × Yea	1	1827.10	1.82	0.089	0.44%
Ele × Si	1	3652.20	3.63	**0.001**	0.88%
Ele × Sea	1	434.79	0.43	0.833	0.10%
Ele × Yea	1	2095.70	2.08	0.060	0.50%
Si × Sea	1	4597.00	4.57	**0.001**	1.10%
Si × Yea	1	2671.80	2.66	**0.009**	0.64%
Sea × Yea	1	8644.90	8.60	**0.001**	2.07%
2HF × 1HF × Ele	1	363.20	0.36	0.861	0.09%
2HF × 1HF × Si	1	1260.70	1.25	0.307	0.30%
2HF × 1HF × Sea	1	3829.80	3.81	**0.002**	0.92%
2HF × 1HF × Yea	1	1284.90	1.28	0.301	0.31%
2HF × Ele × Si	1	790.33	0.79	0.585	0.19%
2HF × Ele × Sea	1	1823.90	1.81	0.093	0.44%
2HF × Ele × Yea	1	1561.60	1.55	0.166	0.37%
2HF × Si × Sea	1	751.33	0.75	0.622	0.18%
2HF × Si × Yea	1	831.52	0.83	0.561	0.20%
2HF × Sea × Yea	1	763.29	0.76	0.654	0.18%
1HF × Ele × Si	1	687.50	0.68	0.663	0.16%
1HF × Ele × Sea	1	841.19	0.84	0.527	0.20%
1HF × Ele × Yea	1	956.70	0.95	0.477	0.23%
1HF × Si × Sea	1	679.12	0.68	0.672	0.16%
1HF × Si × Yea	1	535.46	0.53	0.797	0.13%
1HF × Sea × Yea	1	1960.40	1.95	0.070	0.47%
Ele × Si × Sea	1	2836.80	2.82	**0.007**	0.68%
Ele × Si × Yea	1	1993.00	1.98	0.079	0.48%
Ele × Sea × Yea	1	3734.80	3.71	**0.002**	0.90%
Si × Sea × Yea	1	3183.80	3.17	**0.003**	0.76%
2HF × 1HF × Ele × Si	1	313.16	0.31	0.883	0.08%

2HF × 1HF × Ele × Sea	1	1170.30	1.16	0.353	0.28%
2HF × 1HF × Ele × Yea	1	1594.30	1.59	0.163	0.38%
2HF × 1HF × Si × Sea	1	1698.50	1.69	0.148	0.41%
2HF × 1HF × Si × Yea	1	730.66	0.73	0.650	0.18%
2HF × 1HF × Sea × Yea	1	2071.90	2.06	0.070	0.50%
2HF × Ele × Si × Sea	1	2234.20	2.22	**0.049**	0.54%
2HF × Ele × Si × Yea	1	506.74	0.50	0.779	0.12%
2HF × Ele × Sea × Yea	1	975.93	0.97	0.429	0.23%
2HF × Si × Sea × Yea	1	1253.10	1.25	0.315	0.30%
1HF × Ele × Si × Sea	1	1238.70	1.23	0.328	0.30%
1HF × Ele × Si × Yea	1	741.46	0.74	0.624	0.18%
1HF × Ele × Sea × Yea	1	1924.50	1.91	0.073	0.46%
1HF × Si × Sea × Yea	1	957.80	0.95	0.481	0.23%
Ele × Si × Sea × Yea	1	620.30	0.62	0.735	0.15%
2HF × 1HF × Ele × Si × Sea	1	-17.05	Negative		0.00%
2HF × 1HF × Ele × Si × Yea	1	1337.10	1.33	0.260	0.32%
2HF × 1HF × Ele × Sea × Yea	1	922.28	0.92	0.500	0.22%
2HF × 1HF × Si × Sea × Yea	1	777.91	0.77	0.584	0.19%
2HF × Ele × Si × Sea × Yea	1	473.45	0.47	0.815	0.11%
1HF × Ele × Si × Sea × Yea	1	1274.00	1.27	0.310	0.31%
2HF × 1HF × Ele × Si × Sea × Yea	1	1250.30	1.24	0.290	0.30%
Res	190	191090.00			
Total	253	417120.00			

Appendix 4.4

Field experiment 1, effects of secondary habitat former biomass and type. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed. Data were square-rooted prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	12.46	11.07	**0.001**	5.87%
Secondary habitat former biomass (Bio)	1	1.83	1.63	0.218	0.86%
Site (Si)	1	13.90	12.35	**0.004**	6.55%
Season (Sea)	1	61.27	54.43	**0.001**	28.88%
2HF × Bio	1	3.77	3.35	0.073	1.78%
2HF × Si	1	0.26	0.23	0.640	0.12%
2HF × Sea	1	29.37	26.09	**0.001**	13.84%
Bio × Si	1	4.33	3.85	0.058	2.04%
Bio × Sea	1	5.39	4.78	**0.040**	2.54%
Si × Sea	1	2.56	2.27	0.114	1.21%
2HF × Bio × Si	1	7.06	6.27	**0.018**	3.33%
2HF × Bio × Sea	1	5.49	4.88	**0.032**	2.59%
2HF × Si × Sea	1	6.50	5.78	**0.024**	3.07%
Bio × Si × Sea	1	0.81	0.72	0.406	0.38%
2HF × Bio × Si × Sea	1	3.11	2.77	0.110	1.47%
Res	48	54.04			
Total	63	212.15			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	0.22	2.42	0.128	3.61%
Secondary habitat former biomass (Bio)	1	0.02	0.22	0.644	0.32%
Site (Si)	1	0.08	0.85	0.375	1.27%
Season (Sea)	1	0.00	0.00	0.988	0.00%
2HF × Bio	1	0.16	1.69	0.200	2.53%
2HF × Si	1	0.20	2.18	0.140	3.26%
2HF × Sea	1	0.06	0.62	0.442	0.92%
Bio × Si	1	0.00	0.04	0.880	0.05%
Bio × Sea	1	0.09	1.00	0.324	1.49%
Si × Sea	1	0.40	4.39	**0.044**	6.55%
2HF × Bio × Si	1	0.02	0.21	0.636	0.31%
2HF × Bio × Sea	1	0.12	1.26	0.256	1.87%

2HF × Si × Sea	1	0.37	4.04	0.058	6.02%
Bio × Si × Sea	1	0.00	0.00	0.992	0.00%
2HF × Bio × Si × Sea	1	0.01	0.14	0.727	0.21%
Res	48	4.41			
Total	63	6.15			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	3416	5.20	**0.001**	5.48%
Secondary habitat former biomass (Bio)	1	277	0.42	0.799	0.44%
Site (Si)	1	2006	3.05	**0.015**	3.22%
Season (Sea)	1	7715	11.74	**0.001**	12.38%
2HF × Bio	1	1679	2.56	**0.028**	2.69%
2HF × Si	1	866	1.32	0.275	1.39%
2HF × Sea	1	2871	4.37	**0.002**	4.60%
Bio × Si	1	866	1.32	0.291	1.39%
Bio × Sea	1	803	1.22	0.329	1.29%
Si × Sea	1	4023	6.12	**0.001**	6.45%
2HF × Bio × Si	1	1663	2.53	**0.030**	2.67%
2HF × Bio × Sea	1	743	1.13	0.374	1.19%
2HF × Si × Sea	1	1150	1.75	0.144	1.84%
Bio × Si × Sea	1	1157	1.76	0.128	1.86%
2HF × Bio × Si × Sea	1	1566	2.38	**0.039**	2.51%
Res	48	31543			
Total	63	62341			

Appendix 4.5

Field experiment 2, effects of secondary habitat former morphology across latitudes. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of invertebrates. All factors were treated as fixed and 'Estuary' was nested in 'Latitude'. Data were square-rooted prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	0.94	1.20	0.274	0.21%
Secondary habitat former biomass (Bio)	1	16.25	20.76	**0.001**	3.61%
Primary habitat former (1HF)	1	18.24	23.30	**0.001**	4.05%
Elevation (Ele)	1	0.47	0.61	0.432	0.11%
Latitude (Lat)	2	122.35	78.14	**0.001**	27.19%
Estuary(Latitude) (Est(Lat))	3	37.42	15.93	**0.001**	8.32%
2HF × Bio	1	0.54	0.69	0.408	0.12%
2HF × 1HF	1	0.36	0.46	0.499	0.08%
2HF × Ele	1	1.46	1.87	0.180	0.33%
2HF × Lat	2	9.55	6.10	**0.006**	2.12%
Bio × 1HF	1	0.82	1.05	0.309	0.18%
Bio × Ele	1	0.02	0.02	0.889	0.00%
Bio × Lat	2	2.89	1.85	0.174	0.64%
1HF × Ele	1	8.15	10.41	**0.004**	1.81%
1HF × Lat	2	5.41	3.46	**0.027**	1.20%
Ele × Lat	2	6.70	4.28	**0.014**	1.49%
2HF × Est(Lat)	3	13.66	5.81	**0.003**	3.03%
Bio × Est(Lat)	3	6.96	2.96	**0.040**	1.55%
1HF × Est(Lat)	3	0.75	0.32	0.808	0.17%
Ele × Est(Lat)	3	4.02	1.71	0.176	0.89%
2HF × Bio × 1HF	1	1.39	1.77	0.195	0.31%
2HF × Bio × Ele	1	0.54	0.69	0.448	0.12%
2HF × Bio × Lat	2	4.33	2.77	0.062	0.96%
2HF × 1HF × Ele	1	1.64	2.09	0.133	0.36%
2HF × 1HF × Lat	2	1.08	0.69	0.522	0.24%
2HF × Ele × Lat	2	3.79	2.42	0.096	0.84%
Bio × 1HF × Ele	1	0.27	0.35	0.565	0.06%
Bio × 1HF × Lat	2	1.11	0.71	0.518	0.25%
Bio × Ele × Lat	2	1.93	1.23	0.285	0.43%
1HF × Ele × Lat	2	9.15	5.84	**0.006**	2.03%
2HF × Bio × Est(Lat)	3	1.59	0.68	0.563	0.35%
2HF × 1HF × Est(Lat)	3	0.62	0.26	0.836	0.14%

2HF × Ele × Est(Lat)	3	7.03	2.99	**0.028**	1.56%
Bio × 1HF × Est(Lat)	3	7.80	3.32	**0.022**	1.73%
Bio × Ele × Est(Lat)	3	0.26	0.11	0.953	0.06%
1HF × Ele × Est(Lat)	3	8.74	3.72	**0.013**	1.94%
2HF × Bio × 1HF × Ele	1	0.02	0.03	0.857	0.01%
2HF × Bio × 1HF × Lat	2	0.94	0.60	0.541	0.21%
2HF × Bio × Ele × Lat	2	0.30	0.19	0.844	0.07%
2HF × 1HF × Ele × Lat	2	2.09	1.33	0.282	0.46%
Bio × 1HF × Ele × Lat	2	3.53	2.26	0.108	0.79%
2HF × Bio × 1HF × Est(Lat)	3	1.08	0.46	0.706	0.24%
2HF × Bio × Ele × Est(Lat)	3	1.08	0.46	0.708	0.24%
2HF × 1HF × Ele × Est(Lat)	2	6.40	4.08	**0.026**	1.42%
Bio × 1HF × Ele × Est(Lat)	2	6.71	4.29	**0.023**	1.49%
2HF × Bio × 1HF × Ele × Lat	1	0.86	1.10	0.299	0.19%
2HF × Bio × 1HF × Ele × Est(Lat)	2	2.11	1.35	0.245	0.47%
Res	149	116.65			
Total	240	450.04			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	3.92	26.27	**0.001**	5.28%
Secondary habitat former biomass (Bio)	1	2.68	17.99	**0.001**	3.61%
Primary habitat former (1HF)	1	4.09	27.42	**0.001**	5.51%
Elevation (Ele)	1	0.05	0.33	0.558	0.07%
Latitude (Lat)	2	22.39	75.01	**0.001**	30.13%
Estuary(Latitude) (Est(Lat))	3	1.21	2.70	**0.045**	1.62%
2HF × Bio	1	0.00	0.03	0.877	0.01%
2HF × 1HF	1	0.05	0.31	0.575	0.06%
2HF × Ele	1	0.04	0.25	0.623	0.05%
2HF × Lat	2	1.46	4.89	**0.015**	1.96%
Bio × 1HF	1	0.02	0.12	0.716	0.02%
Bio × Ele	1	0.14	0.91	0.337	0.18%
Bio × Lat	2	0.15	0.50	0.620	0.20%
1HF × Ele	1	1.58	10.62	**0.002**	2.13%
1HF × Lat	2	0.01	0.02	0.988	0.01%
Ele × Lat	2	0.47	1.56	0.220	0.63%
2HF × Est(Lat)	3	0.74	1.65	0.192	1.00%
Bio × Est(Lat)	3	0.50	1.11	0.322	0.67%
1HF × Est(Lat)	3	0.09	0.19	0.906	0.12%
Ele × Est(Lat)	3	2.27	5.06	**0.001**	3.05%
2HF × Bio × 1HF	1	0.30	1.98	0.156	0.40%
2HF × Bio × Ele	1	0.30	2.01	0.184	0.40%
2HF × Bio × Lat	2	0.63	2.09	0.104	0.84%
2HF × 1HF × Ele	1	0.01	0.06	0.821	0.01%
2HF × 1HF × Lat	2	0.12	0.39	0.679	0.16%
2HF × Ele × Lat	2	0.12	0.40	0.676	0.16%
Bio × 1HF × Ele	1	0.39	2.64	0.100	0.53%
Bio × 1HF × Lat	2	0.04	0.12	0.891	0.05%
Bio × Ele × Lat	2	0.21	0.69	0.515	0.28%
1HF × Ele × Lat	2	1.73	5.78	**0.006**	2.32%
2HF × Bio × Est(Lat)	3	0.21	0.48	0.682	0.29%
2HF × 1HF × Est(Lat)	3	0.20	0.44	0.715	0.27%
2HF × Ele × Est(Lat)	3	0.28	0.62	0.616	0.37%
Bio × 1HF × Est(Lat)	3	1.37	3.06	**0.030**	1.84%
Bio × Ele × Est(Lat)	3	0.32	0.70	0.563	0.42%
1HF × Ele × Est(Lat)	3	0.90	2.00	0.102	1.21%
2HF × Bio × 1HF × Ele	1	0.04	0.25	0.620	0.05%
2HF × Bio × 1HF × Lat	2	0.30	1.00	0.389	0.40%
2HF × Bio × Ele × Lat	2	0.18	0.61	0.535	0.25%
2HF × 1HF × Ele × Lat	2	0.36	1.20	0.296	0.48%
Bio × 1HF × Ele × Lat	2	0.30	1.00	0.397	0.40%
2HF × Bio × 1HF × Est(Lat)	3	0.41	0.91	0.467	0.55%

2HF × Bio × Ele × Est(Lat)	3	0.55	1.24	0.307	0.74%
2HF × 1HF × Ele × Est(Lat)	2	0.51	1.70	0.198	0.68%
Bio × 1HF × Ele × Est(Lat)	2	0.09	0.31	0.723	0.13%
2HF × Bio × 1HF × Ele × Lat	1	0.00	0.02	0.888	0.00%
2HF × Bio × 1HF × Ele × Est(Lat)	2	0.41	1.37	0.239	0.55%
Res	149	22.24			
Total	240	74.32			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former type (2HF)	1	7817	7.70	**0.001**	1.53%
Secondary habitat former biomass (Bio)	1	3707	3.65	**0.002**	0.73%
Primary habitat former (1HF)	1	11495	11.33	**0.001**	2.25%
Elevation (Ele)	1	5429	5.35	**0.001**	1.06%
Latitude (Lat)	2	129980	64.03	**0.001**	25.49%
Estuary(Latitude) (Est(Lat))	3	54741	17.98	**0.001**	10.74%
2HF × Bio	1	2277	2.24	**0.026**	0.45%
2HF × 1HF	1	1828	1.80	0.091	0.36%
2HF × Ele	1	2696	2.66	**0.014**	0.53%
2HF × Lat	2	5381	2.65	**0.002**	1.06%
Bio × 1HF	1	1170	1.15	0.337	0.23%
Bio × Ele	1	747	0.74	0.631	0.15%
Bio × Lat	2	2720	1.34	0.197	0.53%
1HF × Ele	1	3612	3.56	**0.002**	0.71%
1HF × Lat	2	11544	5.69	**0.001**	2.26%
Ele × Lat	2	4842	2.39	**0.004**	0.95%
2HF × Est(Lat)	3	8080	2.65	**0.001**	1.58%
Bio × Est(Lat)	3	3540	1.16	0.300	0.69%
1HF × Est(Lat)	3	8441	2.77	**0.001**	1.66%
Ele × Est(Lat)	3	11886	3.90	**0.001**	2.33%
2HF × Bio × 1HF	1	1410	1.39	0.233	0.28%
2HF × Bio × Ele	1	1619	1.60	0.161	0.32%
2HF × Bio × Lat	2	1851	0.91	0.572	0.36%
2HF × 1HF × Ele	1	1479	1.46	0.187	0.29%
2HF × 1HF × Lat	2	3165	1.56	0.095	0.62%
2HF × Ele × Lat	2	2700	1.33	0.187	0.53%
Bio × 1HF × Ele	1	1560	1.54	0.174	0.31%
Bio × 1HF × Lat	2	2017	0.99	0.468	0.40%
Bio × Ele × Lat	2	1803	0.89	0.585	0.35%
1HF × Ele × Lat	2	6867	3.38	**0.001**	1.35%
2HF × Bio × Est(Lat)	3	1692	0.56	0.905	0.33%
2HF × 1HF × Est(Lat)	3	4168	1.37	0.150	0.82%
2HF × Ele × Est(Lat)	3	6210	2.04	**0.009**	1.22%
Bio × 1HF × Est(Lat)	3	5462	1.79	**0.011**	1.07%
Bio × Ele × Est(Lat)	3	3387	1.11	0.366	0.66%
1HF × Ele × Est(Lat)	3	5954	1.96	**0.006**	1.17%
2HF × Bio × 1HF × Ele	1	1165	1.15	0.381	0.23%
2HF × Bio × 1HF × Lat	2	1696	0.84	0.611	0.33%
2HF × Bio × Ele × Lat	2	1381	0.68	0.770	0.27%
2HF × 1HF × Ele × Lat	2	2664	1.31	0.211	0.52%
Bio × 1HF × Ele × Lat	2	2970	1.46	0.118	0.58%
2HF × Bio × 1HF × Est(Lat)	3	3510	1.15	0.317	0.69%

2HF × Bio × Ele × Est(Lat)	3	4052	1.33	0.191	0.79%
2HF × 1HF × Ele × Est(Lat)	2	3222	1.59	0.097	0.63%
Bio × 1HF × Ele × Est(Lat)	2	1678	0.83	0.616	0.33%
2HF × Bio × 1HF × Ele × Lat	1	1991	1.96	0.077	0.39%
2HF × Bio × 1HF × Ele × Est(Lat)	2	1008	0.50	0.890	0.20%
Res	149	151230			
Total	240	509840			

Appendix 4.6

Experiment 3, effects of predation. Chi-square test based on the distribution of *Micrelenchus tenebrosus* in different habitats (M: mud, U: *Ulva* sp., Z: *Zostera muelleri*) and in absence (N) and presence (Y) of the predator. The expected frequencies values took into account the snails missing during the experiments (i.e., values are slightly different across habitats and predation conditions).

OBSERVED FREQUENCIES TABLE

HABITAT	CRAB PRESENCE	M	U	Z	TOT
M	**N**	10.33	0.00	0.00	10.33
M	**Y**	13.00	0.00	0.00	13.00
MU	**N**	5.00	7.33	0.00	12.33
MU	**Y**	3.17	8.83	0.00	12.00
MZ	**N**	0.00	0.00	11.33	11.33
MZ	**Y**	0.00	0.00	10.67	10.67
MZU	**N**	0.00	7.00	4.67	11.67
MZU	**Y**	0.00	6.33	7.00	13.33
TOT		31.50	29.50	33.67	94.67
PROP		0.33	0.31	0.36	1.00

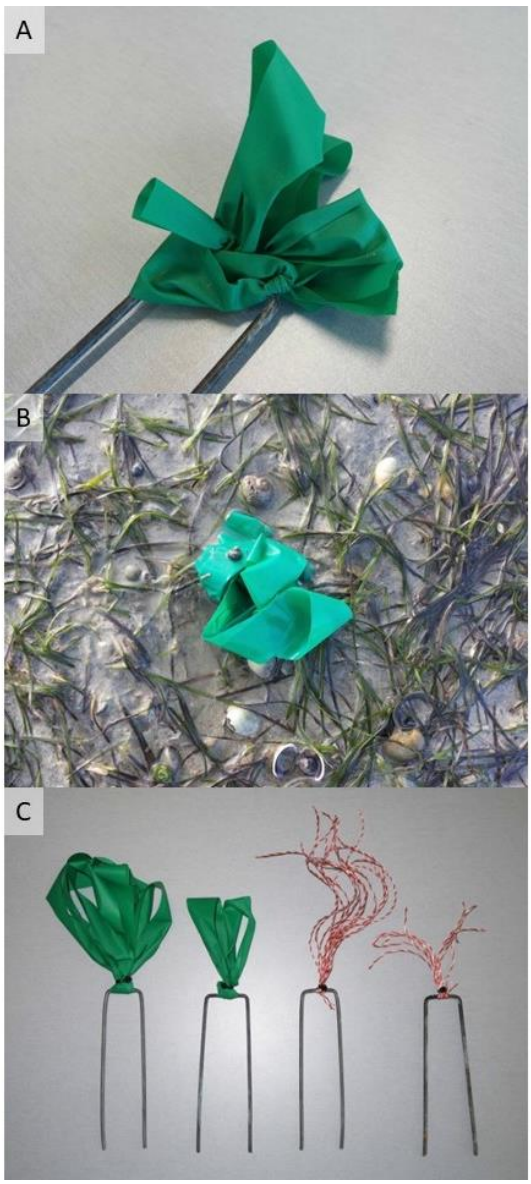
EXPECTED FREQUENCIES TABLE

HABITAT	CRAB PRESENCE	M	U	Z
M	**N**	3.44	3.22	3.67
M	**Y**	4.33	4.05	4.62
MU	**N**	4.10	3.84	4.39
MU	**Y**	3.99	3.74	4.27
MZ	**N**	3.77	3.53	4.03
MZ	**Y**	3.55	3.32	3.79
MZU	**N**	3.88	3.64	4.15
MZU	**Y**	4.44	4.15	4.74

Chi Test	**8E-19**

Appendix 4.7

Mimics used in field experiment 1 (A) and 2 (C). Experiment 1 tested for effect of the secondary habitat former type and biomass. Mimics before (A) and during (B) the experiment. Mimics were made from 2.5 cm wide green flagging tape, cut, twisted and wrapped to provide a shape that mimicked *Ulva* sp., in low and high biomass, and tied to a u-bent 20 cm metal peg that was pushed flush to the sediment. Experiment 2 tested for effects of the secondary habitat former with different morphology across latitudes. Mimics (C) were made from red/white plastic twine (mimicking the branched *Gracilaria chilensis*) and green flagging tape (mimicking the flat *Ulva*, as described in the previous experiment), cut, twisted and wrapped to provide a convenient shape mimicking the seaweeds and tied to a u-bent 20 cm metal peg to be flush into the sediment.



Appendix 4.8

Experiment 3, effects of predation. 36 cages were added between a mudflat and a seagrass bed. Cages were constructed from plastic containers (A, 17×17×18 cm) from which the bottom was removed so that the cage could be pushed into the sediment (A, 12 cm into the sediment, 5 cm protruding above the sediment surface). 36 1-mm holes were drilled in the side-walls of the containers so incoming and outgoing tides would fill and drain the cages following the natural tidal cycle. Each cage enclosed 13 *Micrelenchus tenebrosus* snails (potential crab prey) and then the surface was covered with either mud, *Ulva* sp., *Zostera muelleri* or co-existing *Zostera* and *Ulva*. Finally, 1 predatory crab (*Hemigrapsus crenulatus*) was added to half of all the containers before they were covered with 1-mm mesh to contain the animals (B).

Appendix 5.1

Field experiment 1, testing for the effects of eutrophication and sedimentation on oxidation of silver sticks, seagrass leaves, shoot density, and invertebrates abundances, richness and community structure. Analysis conducted with Permutation based factorial analysis of variance (PERMANOVA). All factors were treated as fixed. Data were square-root transformed prior to analysis.

SILVER STICKS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	600.80	0.82	0.508	6.70%
Sedimentation (Sed)	3	307.23	0.42	0.761	3.43%
Fer × Sed	9	688.21	0.31	0.983	7.68%
Res	30	7366.30			
Total	45	8962.50			

ZOSTERA LEAVES

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	0.05	2.70	0.059	2.28%
Sedimentation (Sed)	3	1.76	102.73	**0.001**	86.88%
Fer × Sed	9	0.04	0.72	0.684	1.82%
Res	32	0.18			
Total	47	2.03			

ZOSTERA SHOOT DENSITY

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	20	0.94	0.468	0.80%
Sedimentation (Sed)	3	2203	105.88	**0.001**	89.27%
Fer × Sed	9	23	0.37	0.933	0.94%
Res	32	222			
Total	47	2468			

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	0.01	0.01	1.000	0.04%
Sedimentation (Sed)	3	15.65	12.01	**0.001**	47.53%
Fer × Sed	9	3.37	0.86	0.559	10.23%
Res	32	13.90			
Total	47	32.93			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	0.16	1.00	0.393	2.45%
Sedimentation (Sed)	3	2.58	15.88	**0.001**	38.68%
Fer × Sed	9	2.19	4.50	**0.001**	32.89%
Res	32	1.73			
Total	47	6.66			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Fertilization (Fer)	3	3956	0.81	0.647	4.91%
Sedimentation (Sed)	3	11441	2.35	**0.005**	14.19%
Fer × Sed	9	13238	0.91	0.639	16.42%
Res	32	51975			
Total	47	80610			

Appendix 5.2

Field experiment 2, testing for effects of sedimentation, drift alga, seagrass, elevation level and season on oxidation of silver sticks, seagrass leaves, shoot density, and invertebrates abundances, richness and community structure. Analysis conducted with Permutation based factorial analysis of variance (PERMANOVA). All factors were treated as fixed. Data were square-root transformed prior to analysis.

SILVER STICKS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	24.72	0.13	0.728	0.23%
Primaryary habitat former (1HF)	1	25.63	0.14	0.718	0.24%
Sedimentation (Sed)	1	395.70	2.14	0.154	3.71%
Elevation (Ele)	1	223.31	1.21	0.266	2.09%
Season (Sea)	1	20.89	0.11	0.743	0.20%
2HF × 1HF	1	197.32	1.07	0.305	1.85%
2HF × Sed	1	286.36	1.55	0.246	2.68%
2HF × Ele	1	158.24	0.86	0.353	1.48%
2HF × Sea	1	92.42	0.50	0.501	0.87%
1HF × Sed	1	17.56	0.09	0.754	0.16%
1HF × Ele	1	1.65	0.01	0.917	0.02%
1HF × Sea	1	218.74	1.18	0.286	2.05%
Sed × Ele	1	8.09	0.04	0.835	0.08%
Sed × Sea	1	167.27	0.90	0.369	1.57%
Ele × Sea	1	80.86	0.44	0.509	0.76%
2HF × 1HF × Sed	1	59.47	0.32	0.580	0.56%
2HF × 1HF × Ele	1	521.65	2.82	0.099	4.89%
2HF × 1HF × Sea	1	145.12	0.78	0.362	1.36%
2HF × Sed × Ele	1	144.94	0.78	0.360	1.36%
2HF × Sed × Sea	1	50.44	0.27	0.618	0.47%
2HF × Ele × Sea	1	2.93	0.02	0.888	0.03%
1HF × Sed × Ele	1	76.00	0.41	0.547	0.71%
1HF × Sed × Sea	1	1.39	0.01	0.936	0.01%
1HF × Ele × Sea	1	5.30	0.03	0.879	0.05%
Sed × Ele × Sea	1	160.57	0.87	0.373	1.50%
2HF × 1HF × Sed × Ele	1	226.06	1.22	0.246	2.12%
2HF × 1HF × Sed × Sea	1	0.36	0.00	0.967	0.00%
2HF × 1HF × Ele × Sea	1	143.17	0.77	0.381	1.34%
2HF × Sed × Ele × Sea	1	6.69	0.04	0.828	0.06%
1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
2HF × 1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
Res	39	7212.60			
Total	68	10675.00			

ZOSTERA LEAVES

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	0.02	2.52	0.128	1.22%
Primaryary habitat former (1HF)	0	0.00	No test		0.00%
Sedimentation (Sed)	1	0.80	105.87	**0.001**	51.19%
Elevation (Ele)	1	0.01	0.98	0.328	0.47%
Season (Sea)	1	0.18	23.48	**0.001**	11.35%
2HF × 1HF	0	0.00	No test		0.00%
2HF × Sed	1	0.02	2.38	0.118	1.15%
2HF × Ele	1	0.01	1.33	0.271	0.64%
2HF × Sea	1	0.00	0.33	0.559	0.16%
1HF × Sed	0	0.00	No test		0.00%
1HF × Ele	0	0.00	No test		0.00%
1HF × Sea	0	0.00	No test		0.00%
Sed × Ele	1	0.01	1.44	0.233	0.70%
Sed × Sea	1	0.25	33.41	**0.001**	16.16%
Ele × Sea	1	0.00	0.01	0.902	0.01%
2HF × 1HF × Sed	0	0.00	No test		0.00%
2HF × 1HF × Ele	0	0.00	No test		0.00%
2HF × 1HF × Sea	0	0.00	No test		0.00%
2HF × Sed × Ele	1	0.00	0.18	0.695	0.09%
2HF × Sed × Sea	1	0.00	0.08	0.785	0.04%
2HF × Ele × Sea	1	0.00	0.12	0.737	0.06%
1HF × Sed × Ele	0	0.00	No test		0.00%
1HF × Sed × Sea	0	0.00	No test		0.00%
1HF × Ele × Sea	0	0.00	No test		0.00%
Sed × Ele × Sea	1	0.02	2.10	0.155	1.02%
2HF × 1HF × Sed × Ele	0	0.00	No test		0.00%
2HF × 1HF × Sed × Sea	0	0.00	No test		0.00%
2HF × 1HF × Ele × Sea	0	0.00	No test		0.00%
2HF × Sed × Ele × Sea	1	0.00	0.56	0.449	0.27%
1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
2HF × 1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
Res	32	0.24			
Total	47	1.57			

ZOSTERA SHOOT DENSITY

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	23.88	6.01	**0.025**	1.60%
Primaryary habitat former (1HF)	0	0.00	No test		0.00%
Sedimentation (Sed)	1	970.67	244.27	**0.001**	65.11%
Elevation (Ele)	1	1.12	0.28	0.608	0.08%
Season (Sea)	1	5.18	1.30	0.249	0.35%
2HF × 1HF	0	0.00	No test		0.00%
2HF × Sed	1	10.49	2.64	0.107	0.70%
2HF × Ele	1	17.76	4.47	**0.049**	1.19%
2HF × Sea	1	0.70	0.18	0.669	0.05%
1HF × Sed	0	0.00	No test		0.00%
1HF × Ele	0	0.00	No test		0.00%
1HF × Sea	0	0.00	No test		0.00%
Sed × Ele	1	5.26	1.32	0.264	0.35%
Sed × Sea	1	314.75	79.21	**0.001**	21.11%
Ele × Sea	1	6.43	1.62	0.210	0.43%
2HF × 1HF × Sed	0	0.00	No test		0.00%
2HF × 1HF × Ele	0	0.00	No test		0.00%
2HF × 1HF × Sea	0	0.00	No test		0.00%
2HF × Sed × Ele	1	9.97	2.51	0.114	0.67%
2HF × Sed × Sea	1	4.16	1.05	0.311	0.28%
2HF × Ele × Sea	1	0.47	0.12	0.734	0.03%
1HF × Sed × Ele	0	0.00	No test		0.00%
1HF × Sed × Sea	0	0.00	No test		0.00%
1HF × Ele × Sea	0	0.00	No test		0.00%
Sed × Ele × Sea	1	0.87	0.22	0.660	0.06%
2HF × 1HF × Sed × Ele	0	0.00	No test		0.00%
2HF × 1HF × Sed × Sea	0	0.00	No test		0.00%
2HF × 1HF × Ele × Sea	0	0.00	No test		0.00%
2HF × Sed × Ele × Sea	1	3.82	0.96	0.349	0.26%
1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
2HF × 1HF × Sed × Ele × Sea	0	0.00	No test		0.00%
Res	29	115.24			
Total	44	1490.80			

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	0.96	1.64	0.201	0.73%
Primaryary habitat former (1HF)	1	0.21	0.36	0.547	0.16%
Sedimentation (Sed)	1	47.08	80.36	**0.001**	36.02%
Elevation (Ele)	1	0.74	1.27	0.245	0.57%
Season (Sea)	1	3.60	6.14	**0.013**	2.75%
2HF × 1HF	1	0.06	0.09	0.762	0.04%
2HF × Sed	1	2.33	3.98	**0.050**	1.79%
2HF × Ele	1	5.85	9.99	**0.005**	4.48%
2HF × Sea	1	2.16	3.69	0.053	1.65%
1HF × Sed	1	7.90	13.48	**0.001**	6.04%
1HF × Ele	1	8.05	13.74	**0.001**	6.16%
1HF × Sea	1	1.17	2.00	0.161	0.90%
Sed × Ele	1	4.64	7.92	**0.007**	3.55%
Sed × Sea	1	3.15	5.37	**0.020**	2.41%
Ele × Sea	1	0.49	0.83	0.359	0.37%
2HF × 1HF × Sed	1	0.01	0.02	0.888	0.01%
2HF × 1HF × Ele	1	0.01	0.01	0.919	0.00%
2HF × 1HF × Sea	1	0.38	0.65	0.414	0.29%
2HF × Sed × Ele	1	0.12	0.20	0.668	0.09%
2HF × Sed × Sea	1	0.48	0.81	0.369	0.36%
2HF × Ele × Sea	1	0.03	0.05	0.823	0.02%
1HF × Sed × Ele	1	0.47	0.80	0.365	0.36%
1HF × Sed × Sea	1	0.29	0.49	0.463	0.22%
1HF × Ele × Sea	1	0.37	0.63	0.437	0.28%
Sed × Ele × Sea	1	0.00	0.00	0.960	0.00%
2HF × 1HF × Sed × Ele	1	2.37	4.04	**0.043**	1.81%
2HF × 1HF × Sed × Sea	1	0.00	0.00	0.998	0.00%
2HF × 1HF × Ele × Sea	1	0.01	0.02	0.894	0.01%
2HF × Sed × Ele × Sea	1	0.14	0.24	0.657	0.11%
1HF × Sed × Ele × Sea	1	0.00	0.00	0.992	0.00%
2HF × 1HF × Sed × Ele × Sea	1	0.14	0.24	0.612	0.11%
Res	64	37.49			
Total	95	130.68			

RICHNESS					
Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Secondary habitat former (2HF)	1	0.00	0.02	0.899	0.01%
Primaryary habitat former (1HF)	1	0.04	0.38	0.539	0.19%
Sedimentation (Sed)	1	8.38	77.58	**0.001**	39.23%
Elevation (Ele)	1	0.00	0.00	0.972	0.00%
Season (Sea)	1	0.30	2.78	0.104	1.41%
2HF × 1HF	1	0.05	0.50	0.497	0.25%
2HF × Sed	1	0.01	0.07	0.771	0.04%
2HF × Ele	1	0.58	5.39	**0.029**	2.73%
2HF × Sea	1	0.10	0.97	0.335	0.49%
1HF × Sed	1	0.37	3.43	0.063	1.73%
1HF × Ele	1	1.94	17.93	**0.001**	9.06%
1HF × Sea	1	0.47	4.35	**0.037**	2.20%
Sed × Ele	1	0.29	2.68	0.111	1.35%
Sed × Sea	1	0.00	0.02	0.889	0.01%
Ele × Sea	1	0.29	2.65	0.104	1.34%
2HF × 1HF × Sed	1	0.09	0.85	0.375	0.43%
2HF × 1HF × Ele	1	0.05	0.47	0.478	0.24%
2HF × 1HF × Sea	1	0.07	0.62	0.413	0.31%
2HF × Sed × Ele	1	0.10	0.91	0.349	0.46%
2HF × Sed × Sea	1	0.25	2.27	0.142	1.15%
2HF × Ele × Sea	1	0.00	0.05	0.841	0.02%
1HF × Sed × Ele	1	0.03	0.29	0.597	0.14%
1HF × Sed × Sea	1	0.00	0.04	0.825	0.02%
1HF × Ele × Sea	1	0.41	3.80	0.058	1.92%
Sed × Ele × Sea	1	0.00	0.00	0.981	0.00%
2HF × 1HF × Sed × Ele	1	0.03	0.27	0.637	0.13%
2HF × 1HF × Sed × Sea	1	0.38	3.53	0.073	1.78%
2HF × 1HF × Ele × Sea	1	0.08	0.75	0.409	0.38%
2HF × Sed × Ele × Sea	1	0.08	0.71	0.394	0.36%
1HF × Sed × Ele × Sea	1	0.05	0.49	0.541	0.25%
2HF × 1HF × Sed × Ele × Sea	1	0.00	0.00	0.954	0.00%
Res	64	6.91			
Total	95	21.37			

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Source	df	SS	Pseudo-F	P(perm)	Contribution
Secondary habitat former (2HF)	1	7515	7.43	**0.001**	4.82%
Primaryary habitat former (1HF)	1	7042	6.96	**0.001**	4.52%
Sedimentation (Sed)	1	20637	20.40	**0.001**	13.24%
Elevation (Ele)	1	2304	2.28	0.052	1.48%
Season (Sea)	1	7358	7.27	**0.001**	4.72%
2HF × 1HF	1	936	0.93	0.510	0.60%
2HF × Sed	1	1853	1.83	0.118	1.19%
2HF × Ele	1	1262	1.25	0.342	0.81%
2HF × Sea	1	1913	1.89	0.091	1.23%
1HF × Sed	1	3702	3.66	**0.002**	2.38%
1HF × Ele	1	3597	3.56	**0.001**	2.31%
1HF × Sea	1	1467	1.45	0.229	0.94%
Sed × Ele	1	3403	3.36	**0.010**	2.18%
Sed × Sea	1	3432	3.39	**0.005**	2.20%
Ele × Sea	1	3042	3.01	**0.019**	1.95%
2HF × 1HF × Sed	1	518	0.51	0.746	0.33%
2HF × 1HF × Ele	1	630	0.62	0.685	0.40%
2HF × 1HF × Sea	1	904	0.89	0.506	0.58%
2HF × Sed × Ele	1	1875	1.85	0.112	1.20%
2HF × Sed × Sea	1	3234	3.20	**0.007**	2.07%
2HF × Ele × Sea	1	1946	1.92	0.105	1.25%
1HF × Sed × Ele	1	601	0.59	0.687	0.39%
1HF × Sed × Sea	1	342	0.34	0.842	0.22%
1HF × Ele × Sea	1	1851	1.83	0.121	1.19%
Sed × Ele × Sea	1	1391	1.37	0.261	0.89%
2HF × 1HF × Sed × Ele	1	708	0.70	0.634	0.45%
2HF × 1HF × Sed × Sea	1	854	0.84	0.549	0.55%
2HF × 1HF × Ele × Sea	1	464	0.46	0.782	0.30%
2HF × Sed × Ele × Sea	1	1199	1.19	0.341	0.77%
1HF × Sed × Ele × Sea	1	2774	2.74	**0.020**	1.78%
2HF × 1HF × Sed × Ele × Sea	1	2359	2.33	**0.044**	1.51%
Res	64	64744			
Total	95	155860			

Appendix 6.1

Spatial survey, effects of primary and secondary habitat formers. List of treatments and relative replicates in the different locations and reefs and relative replicates (+/-: presence/absence of epiphyte, T: *Cystophora torulosa*, S: *C. scalaris*, R: *C. retroflexa*).

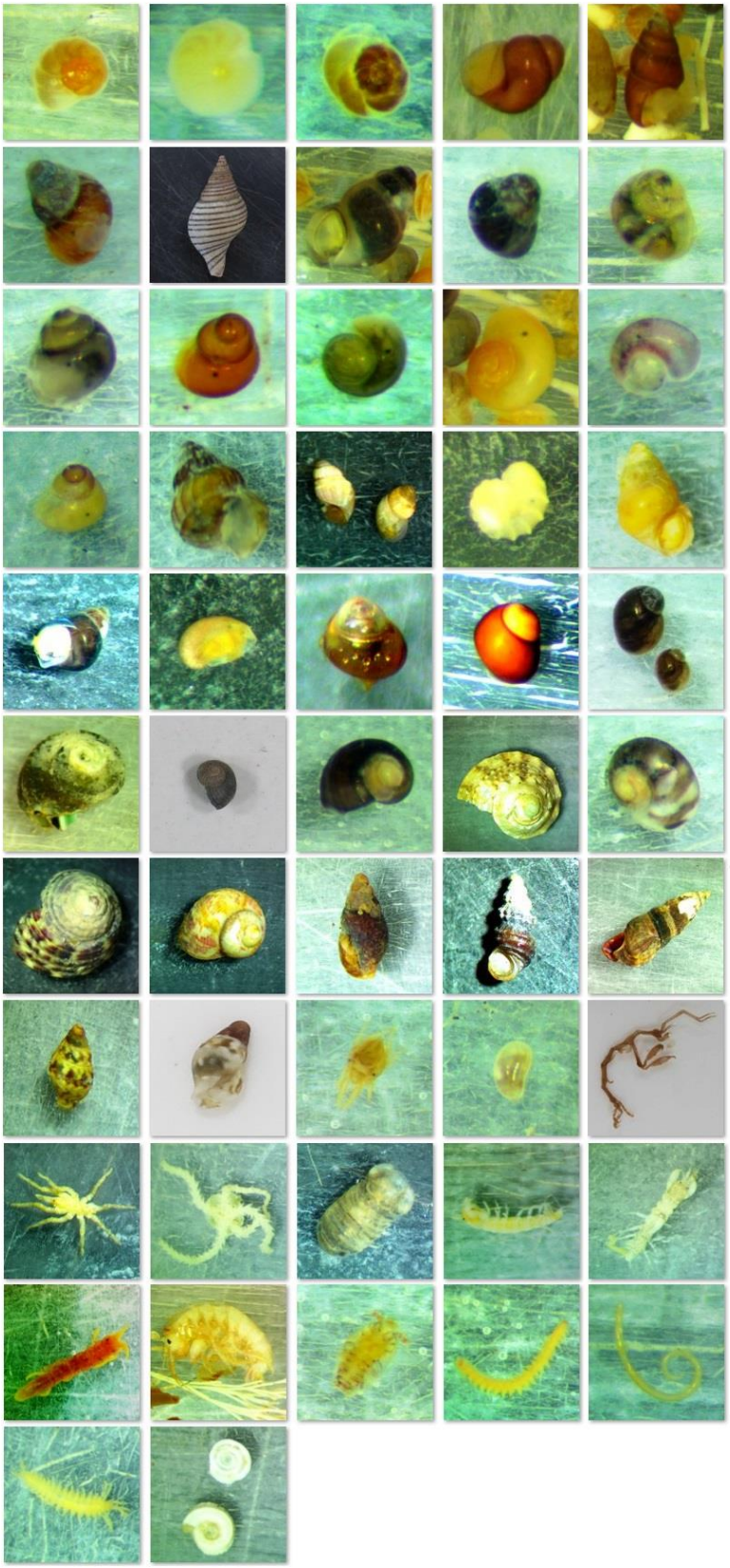
LATITUDE	MORAKI										PILE BAY										KAIKOURA										CAPE CAMPBELL									
DATES	05/11/2014 to 09/11/2014										30/11/2014 to 20/02/2015										03/12/2014 to 04/12/2014										28/01/2015 to 28/01/2015									
GEOCOORDINATES	45°21'25.8"S 170°51'44.8"E							45°21'52.4"S 170°51'47.5"E			43°37'05.4"S 172°45'48.7"E							43°37'15.6"S 172°45'18.0"E			42°25'09.9"S 173°42'36.2"E							42°25'53.0"S 173°41'28.0"E							41°44'31.9"S 174°16'33.5"E							41°43'27.6"S 174°16'39.3"E						
REEF	POINT							KAIK			REEF 1							REEF 2			WAIREPO							SOUTH BAY							REEF 1							REEF 2						
EPIPHYTISMS	R-	R+	S-	S+	T-	T+		R-	R+	S-	S+	T-	T+		R-	R+	S-	S+	T-	T+	R-	R+	S-	S+	T-	T+		R-	R+	S-	S+	T-	T+		R-	R+	S-	S+	T-	T+	
REPLICATES	5	6	3	4	3	6		4	4	4	8	3	3		4	1	4	13	3	6	0	0	4	4	4	1		4	3	3	3	4	7		2	3	3	8	3	7		3	0	4	12	3	3		0	0	4	7	3	3	
Entagled seaweeds	-	6	-	4	-	6		-	4	-	8	-	3		-	1	-	13	-	6	-	-	-	4	-	1		4	3	-	3	-	7		-	3	-	8	-	7		-	-	-	12	-	3		-	-	-	7	-	3	112
Jania micrarthrodia	-	6	-	4	-	6		-	4	-	5	-	2		-	-	-	-	-	-	-	-	-	-	-	-		-	1	-	1	-	5		-	-	-	-	-	1		-	2	-	1	-	3		-	-	-	3	-	1	42
Lophothamnion hirtum	-	1	-	3	-	1		-	1	-	6	-	3		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	-	-	-		-	-	-	3	-	-	19
Hymenena sp.	-	-	-	1	-	-		-	-	-	1	-	-		-	3	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	1	-	-		-	-	-	1	-	-	8
Cladpsenia oblongifolia	-	-	-	1	-	-		-	1	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	1	-	3		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	2
Coutlina ofiinalis	-	-	-	-	-	-		-	1	-	1	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	1	-	1	-	3		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	7
Ploamium mirtuladinales	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	1	-	-	-	-		-	-	-	-	-	-		-	2	-	-	-	-		-	-	-	-	-	-	3
Bryozoa	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	0
Cyanobacteria	-	-	1	-	-	-		-	-	1	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	1	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	4
Unidentified sp.1	-	-	1	-	-	-		-	-	1	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	2
Premadalia cf. *capillacea*	-	-	-	-	-	-		-	-	1	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.2	-	-	2	-	-	-		-	-	-	-	1	-		1	-	5	-	2	-	-	-	-	-	-	-		-	-	1	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	12
Echinothamnion sp.	-	-	-	-	-	-		3	-	-	-	1	-		-	1	-	-	-	-	-	-	-	-	-	-		-	-	-	-	1	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	3	-	1	11
Haliptilon roseum	-	-	-	-	-	-		-	1	-	-	-	-		-	-	-	1	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Halopteris sp.	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Halopteris congesta	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Colpomenia sp.	-	-	-	-	-	-		-	1	-	-	-	-		1	-	9	-	6	-	-	-	-	1	-	-		-	1	-	-	-	1		-	-	-	1	-	-		-	1	-	-	-	-		-	-	-	-	-	-	21
Polyiphonia sp.	-	-	-	-	-	-		-	1	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	1	-	-	-	-		-	-	-	1	-	4		-	-	-	-	-	-		-	-	-	1	-	-	10
Polyiphonia cf. *atertima*	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	1	-	-	-	2		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	3
Champia novae-zelandiae	-	-	-	-	-	-		-	-	-	-	-	-		-	3	-	-	-	-	-	-	-	1	-	-		-	-	1	-	3	-		-	-	-	-	-	1		-	-	-	-	-	-		-	-	-	1	-	-	11
Chaetomorpha sp.	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	1	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.3	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.4	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Ulva sp.	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	1	-	-		-	-	-	-	-	-	2
Umitia cf. *cuspitosa*	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	1	-	-		-	-	-	-	-	-	1
Lindaraxine hinghamiae	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Xiphophammis australis	-	-	-	-	-	-		-	-	-	-	-	-		-	1	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Ecteocarpus sp.	-	-	-	-	-	-		-	-	-	-	-	-		-	1	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Dictyota cf. *elegans*	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Callophyllis hombroniana	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	3	-	-		-	-	-	-	-	-	3
Caulerpa brownii	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	2	-	1		-	-	-	-	-	-	3
Cladostephus spongiosus	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	-	-	-	1
Balita callitricha	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-		-	-	-	-	-	-	1
Codium dimorphum	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	1	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.5	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	2	-	-		-	-	-	1	-	-	3
Unidentified sp.6	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	3
Unidentified sp.7	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.8	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.9	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	2
Unidentified sp.10	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	1	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.11	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1
Unidentified sp.12	-	-	-	-	-	-		-	-	-	-	-	-		1	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	1

Appendix 6.2

Experiment 2, effects of secondary habitat former biomass and type. Photos of the studied primary (A: *Cystophora retroflexa*, B: *C. torulosa*, C: *C. scalaris*) and secondary (D: *Jania micrarthrodia*, E: *Polysiphonia decipiens*, F: epiphyte mimic) habitat formers.

Appendix 6.3

Photos of the most common morpho-species.



Appendix 6.4

Spatial survey, effects of primary and secondary habitat formers across latitudes. Permutation based factorial analysis of variance was used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of gastropods. All factors were treated as fixed and 'Reef' was nested in 'Latitude'. Data were standardized per dry weight of the total seaweed association and square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Latitude (Lat)	3	87	8.18	**0.001**	6.66%
1st HF (1HF)	2	83	11.64	**0.001**	6.32%
2nd HF (2HF)	1	103	28.90	**0.001**	7.85%
Reef(Latitude) Ree(Lat)	4	120	8.42	**0.001**	9.15%
Lat × 1HF	6	29	1.34	0.247	2.19%
Lat × 2HF	3	4	0.39	0.767	0.32%
1HF × 2HF	2	12	1.75	0.177	0.95%
Ree(Lat) × 1HF	6	52	2.43	**0.036**	3.95%
Ree(Lat) × 2HF	4	26	1.85	0.140	2.01%
Lat × 1HF × 2HF	5	43	2.43	**0.039**	3.30%
Ree(Lat) × 1HF × 2HF	6	26	1.20	0.298	1.96%
Res	146	519			
Total	188	1309			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Latitude (Lat)	3	18.10	23.29	**0.001**	20.53%
1st HF (1HF)	2	2.81	5.43	**0.012**	3.19%
2nd HF (2HF)	1	0.35	1.36	0.243	0.40%
Reef(Latitude) Ree(Lat)	4	8.63	8.33	**0.001**	9.79%
Lat × 1HF	6	2.76	1.78	0.116	3.13%
Lat × 2HF	3	0.11	0.14	0.928	0.12%
1HF × 2HF	2	0.49	0.95	0.369	0.56%
Ree(Lat) × 1HF	6	0.83	0.53	0.777	0.94%
Ree(Lat) × 2HF	4	2.85	2.75	**0.035**	3.24%
Lat × 1HF × 2HF	5	0.81	0.63	0.662	0.92%
Ree(Lat) × 1HF × 2HF	6	0.64	0.41	0.866	0.73%
Res	146	37.83			
Total	188	88.18			

COMMUNITY STRUCTURE					
Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Latitude (Lat)	3	57997	14.99	**0.001**	14.53%
1st HF (1HF)	2	5967	2.31	**0.001**	1.49%
2nd HF (2HF)	1	9409	7.29	**0.001**	2.36%
Reef(Latitude) Ree(Lat)	4	38568	7.48	**0.001**	9.66%
Lat × 1HF	6	11805	1.53	**0.004**	2.96%
Lat × 2HF	3	9277	2.40	**0.001**	2.32%
1HF × 2HF	2	3198	1.24	0.185	0.80%
Ree(Lat) × 1HF	6	9525	1.23	0.113	2.39%
Ree(Lat) × 2HF	4	9662	1.87	**0.001**	2.42%
Lat × 1HF × 2HF	5	7408	1.15	0.229	1.86%
Ree(Lat) × 1HF × 2HF	6	10272	1.33	**0.036**	2.57%
Res	146	188320			
Total	188	399290			

Appendix 6.5

Experiment 1, effects of primary and secondary habitat formers across seasons. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of gastropods. All factors were treated as fixed. Data were standardized per dry weight of the total seaweed association and square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Season (Sea)	1	186	39.58	**0.001**	28.59%
1st HF (1HF)	2	71	7.51	**0.002**	10.84%
2nd HF (2HF)	2	116	12.30	**0.001**	17.77%
Sea × 1HF	2	44	4.72	**0.014**	6.82%
Sea × 2HF	2	32	3.45	**0.036**	4.98%
1HF × 2HF	4	11	0.58	0.654	1.68%
Sea × 1HF × 2HF	4	35	1.84	0.143	5.33%
Res	47	221			
Total	64	650			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Season (Sea)	1	7.6	43.42	**0.001**	28.74%
1st HF (1HF)	2	2.9	8.32	**0.003**	11.01%
2nd HF (2HF)	2	1.9	5.53	**0.006**	7.32%
Sea × 1HF	2	0.9	2.70	0.072	3.58%
Sea × 2HF	2	0.8	2.21	0.107	2.92%
1HF × 2HF	4	0.7	1.01	0.416	2.66%
Sea × 1HF × 2HF	4	1.8	2.53	**0.048**	6.69%
Res	47	8.3			
Total	64	26.5			

COMMUNITY STRUCTURE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Season (Sea)	1	25494	19.12	**0.001**	22.28%
1st HF (1HF)	2	3123	1.17	0.260	2.73%
2nd HF (2HF)	2	7115	2.67	**0.001**	6.22%
Sea × 1HF	2	2410	0.90	0.571	2.11%
Sea × 2HF	2	3479	1.30	0.163	3.04%
1HF × 2HF	4	4324	0.81	0.808	3.78%
Sea × 1HF × 2HF	4	4043	0.76	0.879	3.53%
Res	47	62658			
Total	64	114440			

Appendix 6.6

Experiment 2a, effects of secondary habitat former biomass and type across seasons on *Cystophora scalaris*. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of gastropods. All factors were treated as fixed. Data were standardized per dry weight of the total seaweed association and square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Season (Sea)	1	63.24	11.63	**0.002**	12.14%
Reef (Ree)	1	11.71	2.15	0.158	2.25%
2nd HF type (Typ)	1	18.71	3.44	0.080	3.59%
2nd HF biomass (Bio)	1	28.81	5.30	**0.019**	5.53%
Sea × Ree	1	0.18	0.03	0.845	0.03%
Sea × Typ	1	0.03	0.01	0.941	0.01%
Sea × Bio	1	6.29	1.16	0.265	1.21%
Ree × Typ	1	84.84	15.61	**0.001**	16.28%
Ree × Bio	1	0.05	0.01	0.925	0.01%
Typ × Bio	1	18.28	3.36	0.072	3.51%
Sea × Ree × Typ	1	9.14	1.68	0.201	1.75%
Sea × Ree × Bio	1	0.03	0.00	0.950	0.00%
Sea × Typ × Bio	1	17.38	3.20	0.085	3.33%
Ree × Typ × Bio	1	0.03	0.01	0.935	0.01%
Sea × Ree × Typ × Bio	1	2.34	0.43	0.518	0.45%
Res	43	233.74			
Total	58	520.99			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Season (Sea)	1	0.81	20.29	**0.001**	15.32%
Reef (Ree)	1	0.16	3.89	0.059	2.94%
2nd HF type (Typ)	1	2.58	64.16	**0.001**	48.45%
2nd HF biomass (Bio)	1	0.51	12.63	**0.004**	9.54%
Sea × Ree	1	0.10	2.45	0.117	1.85%
Sea × Typ	1	0.09	2.20	0.143	1.66%
Sea × Bio	1	0.11	2.86	0.107	2.16%
Ree × Typ	1	0.28	6.94	**0.012**	5.24%
Ree × Bio	1	0.13	3.19	0.079	2.41%
Typ × Bio	1	0.00	0.04	0.836	0.03%
Sea × Ree × Typ	1	0.05	1.33	0.251	1.00%

Sea × Ree × Bio	1	0.13	3.17	0.083	2.40%
Sea × Typ × Bio	1	0.01	0.15	0.698	0.11%
Ree × Typ × Bio	1	0.06	1.51	0.196	1.14%
Sea × Ree × Typ × Bio	1	0.00	0.02	0.910	0.01%
Res	43	1.73			
Total	58	5.32			

COMMUNITY STRUCTURE

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Season (Sea)	1	10974	10.38	**0.001**	12.92%
Reef (Ree)	1	9205	8.71	**0.001**	10.83%
2nd HF type (Typ)	1	2558	2.42	**0.010**	3.01%
2nd HF biomass (Bio)	1	1335	1.26	0.209	1.57%
Sea × Ree	1	2441	2.31	**0.007**	2.87%
Sea × Typ	1	1015	0.96	0.483	1.19%
Sea × Bio	1	1524	1.44	0.147	1.79%
Ree × Typ	1	2424	2.29	**0.014**	2.85%
Ree × Bio	1	664	0.63	0.785	0.78%
Typ × Bio	1	1262	1.19	0.289	1.48%
Sea × Ree × Typ	1	595	0.56	0.857	0.70%
Sea × Ree × Bio	1	743	0.70	0.738	0.87%
Sea × Typ × Bio	1	1171	1.11	0.330	1.38%
Ree × Typ × Bio	1	796	0.75	0.720	0.94%
Sea × Ree × Typ × Bio	1	459	0.43	0.940	0.54%
Res	43	45467			
Total	58	84964			

Appendix 6.7

Experiment 2b, effects of secondary habitat former biomass and type on *Hormosira banksii*. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of gastropods. All factors were treated as fixed. Data were standardized per dry weight of the total seaweed association and square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Reef (Ree)	1	2083	12.26	**0.001**	26.34%
2nd HF type (Typ)	1	57	0.34	0.731	0.72%
2nd HF biomass (Bio)	1	1488	8.76	**0.001**	18.82%
Ree × Typ	1	337	1.98	0.148	4.26%
Ree × Bio	1	392	2.31	0.099	4.96%
Typ × Bio	1	61	0.36	0.702	0.77%
Reef (Ree)	1	396	2.33	0.092	5.01%
Res	18	3059			
Total	25	7908			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Reef (Ree)	1	0.02	0.27	0.610	1.41%
2nd HF type (Typ)	1	0.01	0.10	0.765	0.55%
2nd HF biomass (Bio)	1	0.01	0.20	0.653	1.06%
Ree × Typ	1	0.01	0.15	0.718	0.80%
Ree × Bio	1	0.00	0.05	0.833	0.26%
Typ × Bio	1	0.00	0.02	0.886	0.10%
Reef (Ree)	1	0.00	0.07	0.799	0.39%
Res	18	1.17			
Total	25	1.22			

COMMUNITY STRUCTURE					
Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Reef (Ree)	1	78	11.01	**0.001**	25.64%
2nd HF type (Typ)	1	27	3.76	**0.005**	8.76%
2nd HF biomass (Bio)	1	40	5.68	**0.002**	13.22%
Ree × Typ	1	16	2.33	0.052	5.42%
Ree × Bio	1	6	0.87	0.491	2.02%
Typ × Bio	1	14	2.03	0.090	4.72%
Reef (Ree)	1	15	2.14	0.069	4.99%
Res	18	128			
Total	25	304			

Appendix 6.8

Comparison between *Cystophora scalaris* and *Hormosira banksii* in experiments 2a-2b. Permutation based factorial analysis of variance used to determine the contribution of each test factor to the variability of the habitat cascade tested on total abundance, taxonomic richness and community structure of gastropods. All factors were treated as fixed. Data were standardized per dry weight of the total seaweed association and square-root transformed prior to analysis.

ABUNDANCE

Source	df	SS	Pseudo-F	P(perm)	Contribution
Reef (Ree)	1	40.9	14.16	**0.002**	9.14%
1st HF (1HF)	1	96.2	33.28	**0.001**	21.49%
2nd HF type (Typ)	1	3.4	1.17	0.264	0.76%
2nd HF biomass (Bio)	1	32.0	11.06	**0.003**	7.14%
Ree x 1HF	1	12.7	4.38	**0.040**	2.83%
Ree x Typ	1	67.9	23.50	**0.001**	15.18%
Ree x Bio	1	0.0	0.00	0.981	0.00%
1HF x Typ	1	5.9	2.03	0.149	1.31%
1HF x Bio	1	8.7	3.01	0.094	1.94%
Typ x Bio	1	1.4	0.48	0.487	0.31%
Ree x 1HF x Typ	1	11.1	3.83	0.066	2.47%
Ree x 1HF x Bio	1	0.2	0.06	0.798	0.04%
Ree x Typ x Bio	1	11.5	3.97	0.061	2.56%
1HF x Typ x Bio	1	1.6	0.56	0.445	0.36%
Ree x 1HF x Typ x Bio	1	4.4	1.54	0.234	0.99%
Res	37	106.9			
Total	52	447.6			

RICHNESS

Source	df	SS	Pseudo-F	P(perm)	Contribution
Reef (Ree)	1	0.06	1.18	0.276	1.46%
1st HF (1HF)	1	0.50	9.75	**0.004**	12.11%
2nd HF type (Typ)	1	0.91	17.95	**0.002**	22.29%
2nd HF biomass (Bio)	1	0.18	3.45	0.077	4.28%
Ree x 1HF	1	0.18	3.55	0.062	4.41%
Ree x Typ	1	0.08	1.66	0.198	2.07%
Ree x Bio	1	0.14	2.78	0.112	3.45%
1HF x Typ	1	0.71	13.97	**0.001**	17.35%
1HF x Bio	1	0.33	6.49	**0.016**	8.06%
Typ x Bio	1	0.00	0.03	0.865	0.04%
Ree x 1HF x Typ	1	0.18	3.58	0.058	4.44%

Ree x 1HF x Bio	1	0.09	1.76	0.197	2.19%
Ree x Typ x Bio	1	0.02	0.45	0.501	0.56%
1HF x Typ x Bio	1	0.00	0.00	0.982	0.00%
Ree x 1HF x Typ x Bio	1	0.00	0.06	0.806	0.08%
Res	37	1.88			
Total	52	4.10			

COMMUNITY STRUCTURE

Source	**df**	**SS**	**Pseudo-F**	**P(perm)**	**Contribution**
Reef (Ree)	1	5522	5.96	**0.001**	4.81%
1st HF (1HF)	1	48156	51.95	**0.001**	41.97%
2nd HF type (Typ)	1	2027	2.19	**0.021**	1.77%
2nd HF biomass (Bio)	1	1694	1.83	0.060	1.48%
Ree x 1HF	1	4009	4.32	**0.001**	3.49%
Ree x Typ	1	1876	2.02	**0.045**	1.64%
Ree x Bio	1	982	1.06	0.414	0.86%
1HF x Typ	1	1664	1.80	0.061	1.45%
1HF x Bio	1	1182	1.27	0.237	1.03%
Typ x Bio	1	541	0.58	0.807	0.47%
Ree x 1HF x Typ	1	877	0.95	0.479	0.76%
Ree x 1HF x Bio	1	771	0.83	0.568	0.67%
Ree x Typ x Bio	1	566	0.61	0.787	0.49%
1HF x Typ x Bio	1	829	0.89	0.488	0.72%
Ree x 1HF x Typ x Bio	1	917	0.99	0.485	0.80%
Res	37	34300			
Total	52	114730			

Appendix 6.9

Laboratory grazing experiment. Permutation based factorial analysis of variance based on the percentage of biomass lost. All factors were treated as fixed.

Source	df	SS	Pseudo-F	P(perm)	Contribution
Grazers (Gra)	1	5	0.18	0.657	0.10%
2nd habitat former (2HF)	2	635	11.39	**0.001**	13.06%
1st habitat former (1HF)	3	283	3.39	**0.023**	5.83%
Season (Sea)	1	1	0.05	0.830	0.03%
Gra x 2HF	2	65	1.16	0.327	1.34%
Gra x 1HF	3	115	1.38	0.277	2.38%
Gra x Sea	1	22	0.79	0.401	0.45%
2HF x 1HF	5	350	2.52	**0.03**	7.21%
2HF x Sea	2	68	1.22	0.286	1.40%
1HF x Sea	3	173	2.07	0.104	3.57%
Gra x 2HF x 1HF	5	286	2.05	0.082	5.88%
Gra x 2HF x Sea	2	9	0.15	0.857	0.18%
Gra x 1HF x Sea	3	65	0.78	0.511	1.34%
2HF x 1HF x Sea	5	183	1.31	0.273	3.77%
Gra x 2HF x 1HF x Sea	5	147	1.05	0.363	3.02%
Res	88	2451			
Total	131	4858			